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Distribution of deep-sea invertebrate megafauna off Central California

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**DISTRIBUTION OF DEEP-SEA INVERTEBRATE MEGAFUNA
OFF CENTRAL CALIFORNIA**

**A Thesis
Presented To
The Faculty of Moss Landing Marine Laboratories
San Jose State University**

**In Partial Fulfillment
of the Requirements for the Degree
Master of Science**

**By
Susan Craig
December 1997**

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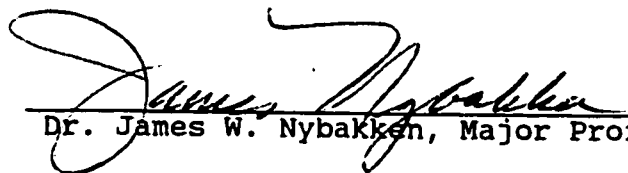
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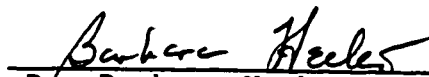
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DISTRIBUTION OF DEEP-SEA INVERTEBRATE MEGAFUNA
OFF CENTRAL CALIFORNIA

by Susan Craig

Otter and beam trawls were used to sample the invertebrate benthic megafauna between 2300-3300 m at three sites along the central California coast between the Farallon Islands and Point Sur. Echinodermata was the dominant phylum in trawls at all sites, with Holothuroidea being the dominant echinoderm class. In general, relative abundances of species and faunal similarities varied among sites, with the greatest differences occurring between sites that were farthest apart. Trawls taken in summer and in winter at the Farallon site demonstrated some seasonal difference in species composition, but most differences in species composition were probably due to different depths covered, competition, and patchiness.

A camera sled was used to sample invertebrate epibenthic megafauna between 2300-3075 m near the Farallon Islands, California. Cnidaria was the dominant phylum seen in the camera sled photographs, with Pennatulacea being the dominant cnidarian order. Mean abundances of invertebrate taxa estimated from camera sled photographs were much greater than those estimated in trawls.

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INTRODUCTION

The relatively few deep-sea studies in the eastern Pacific have focussed primarily on areas off the Oregon coast (Alton 1972; Carney & Carey 1976 & 1982; Carey *et al.* 1990) and off southern California (Hartman & Barnard 1958; Rokop 1974; Smith & Hamilton 1983; Smith 1985a). Until recently, the deep-sea invertebrate benthic community off the central Californian coast remained largely unstudied with little reported data available (see Summers 1993). In the early 1990's a Navy grant enabled sampling to be done of the invertebrate megafauna in three areas off the central California coast. This thesis summarizes the results from sampling near the Farallon Islands in the summer of 1991 and winter of 1992, as well as sampling near Pioneer Canyon and in Monterey Canyon in the winter of 1992. In these surveys trawls were used to sample a depth range from approximately 2300 to 3300 m. Also, camera sled transects were conducted at the Farallon site in the summer of 1991.

Initial results from these surveys were published in two reports prepared for the U.S. Navy and PRC Environmental Management, Inc. (Nybakken *et al.* 1992ab). This thesis differs from these reports in a number of ways: (1) More species have been identified in the interim. (2) Polychaetes from the Farallon site in 1991, which were not identified in the 1992a report, have been included. (3)

Invertebrate mean abundances cited in the 1992a report were incorrect and have been corrected herein. (4) Cumulative species curves in this thesis are based on more repetitions than those in either the 1992a or 1992b reports. (5) The species list in the 1992b report did not separate out species by site; a species presence table in this thesis does so. (6) Trawl data from the 1992a and 1992b reports were primarily reported as mean abundances of species in rank order, with little graphic analysis. In this thesis the trawl data were used to graphically analyze the major taxonomic groupings (classes, orders, etc.) and the relative abundances and mean abundances were calculated for each species and taxon respectively. (7) Percent similarities calculated in the 1992b report were based on mean abundances, which often have a high level of variability. Percent similarities in this thesis are based on relative abundances and the method used is one of the most conservative quantitative similarity coefficients available and is relatively unaffected by sample size or species diversity (Wolda 1981; Krebs 1989). Also, the polychaetes from the Farallon 1991 trawls were included in these percent similarity calculations. Percent similarity between the Farallon 1991 and Farallon 1992 trawls was also calculated for the 25 most common species collected in the Farallon 1991 trawls. This was not done in the 1992b report.

Percent similarity was calculated to compare taxa (e.g., pennatulaceans, holothurians, etc.) in camera sled photographs to similar taxa in trawls. This also was not done in the 1992b report. (8) Tables have been created listing species which were collected at only one site and species which were collected at all sites. (9) Correctly adjusted lower mean abundances from trawls were used to compare the 18 taxa identified in the camera sled photographs and also collected in trawls. (10) Spearman's rank and graphic analyses were used to compare mean abundance of taxa (e.g., sea pens, anemones, etc.) estimated from the camera sled and from trawls. This was not done in the 1992b report.

The specific objectives of this thesis were: (1) to characterize the invertebrate megafaunal population at the base of the continental slope off central California using relative and mean abundances; (2) to compare species similarity among three sites; (3) to compare species composition and relative abundance in summer versus winter at one site and; (4) to compare abundance and composition of benthic invertebrate megafauna between two sampling methods.

METHODS AND MATERIALS

Background

The data used in this study were collected during a series of studies conducted for the U.S. Navy and the Environmental Protection Agency through PRC Environmental Management, Inc. to characterize the benthic invertebrate megafauna at a site proposed for dredge material disposal. This U.S. Navy Ocean Disposal Site (NODS) is located on the continental slope off central California near the Farallon Islands, within the Chemical Munitions Dumping Area (CMDA). The studies examined biological, sedimentary, chemical, and physical features of this deep-sea area and resulted in four reports (Blake et al. 1992; Hecker Environmental Consulting 1992; Nybakken et al. 1992ab).

Study Locations

The primary sampling site (Farallon site) is approximately 40 nm W/SW of San Francisco Bay in depths of approximately 2300 to 3075 m. Otter and beam trawls and camera sled sampling took place within the Navy Ocean Disposal Site (NODS), a target area in the southwestern corner of the Chemical Munitions Dumping Area measuring 2 minutes of latitude by 2 minutes of longitude. This sampling area will be referred to as the Farallon site (Table 1; Figures 1 and 2).

Two additional sites were sampled: an area SW of Pioneer Canyon which is 56 km south of the Farallon site, and an area on the fan of Monterey Canyon, approximately 145 km south of the Farallon site and approximately 48 nm SW of Moss Landing, Ca. These sites will be referred to as the Pioneer Canyon site and the Monterey Canyon site respectively (Table 2 and Figure 3).

Trawl Sampling

Trawl sampling was conducted at all sites. Trawls were taken between July 26 and 31, 1991 at the Farallon site and between February 27 and March 3, 1992 at the Farallon, Pioneer Canyon, and Monterey Canyon sites.

The beam trawl had a mouth opening of 2.1 m and a bag length of 6.7 m. The mesh was made of #60 nylon seine twine of 3.8 cm stretch mesh with a black net preservative. A Benthos pinger was attached to the trawl cable 25 meters ahead of the trawl cable. Any change in depth during the trawl was compensated for by adjusting the tension on the cable to keep the pinger and bottom traces on the Precision Depth Recorder (PDR) 25 meters apart. Beam trawl deployment was the same for all tows: the trawl's progress was monitored by the trace from a pinger on the PDR. Position of the ship was determined by the ship's Global Positioning System when the trawl was engaged on the bottom and when the

trawl left the bottom for its ascent. Bottom time of the trawls ranged from 24 to 66 minutes. Position of the net on the bottom, amount of line out, depth, and line tension were recorded throughout each trawl.

In late July 1991 16 benthic trawls were taken from the R/V Wecoma at depths of 2300-3075 m at the Farallon site. Trawling was concentrated around the NODS site over a one-week sampling period. Twelve trawls were beam trawls and four were otter trawls (a standard commercial otter trawl with a 40-ft. foot rope and weighted aluminum doors was used). All 12 beam trawls successfully engaged the bottom, but one was jettisoned with the net when it was found to contain a radioactive object. Only two otter trawls were successful at returning samples (Table 1).

In February/March 1992 four successful beam trawls were taken from the R/V Point Sur at the Farallon site between 2850 and 3000 m, four at the Pioneer Canyon site between 3090 and 3300 m, and eight at the Monterey Canyon site between 2620 and 3270 m (Table 2).

The specimens were sorted into higher taxa on board the ship and preserved in 10% buffered formalin. One week later specimens were transferred to a water bath for 24 hours and then preserved in 70% ethanol. Later in the laboratory, specimens were identified to the lowest possible taxon. They then were distributed to experts in the field for

verification of identifications.

Because the area sampled per trawl varied widely, ranging from 1867 m² to 19,793 m², all trawl sample data were standardized to number of individuals per 100 m². To determine the total area sampled per trawl, latitude and longitude readings were taken when the trawl first engaged the bottom and when it left the bottom for its ascent. This distance was multiplied by the width of the beam. This area was then converted to units of 100 m².

Camera Sled Sampling

Camera sled transects were conducted at the Farallon site in July 1991, one week before the same site was sampled by trawls. Sections of these camera sled transects overlapped certain trawled areas, allowing for comparisons to be made regarding the mean and relative abundances of certain invertebrate taxa. These two sampling methods resulted in sufficient data to characterize the dominant organisms of the deep-sea benthic invertebrate community.

Camera sled sampling at the Farallon site during July 1991 used two towed camera sleds (Hecker Environmental Consulting 1992). The frames of the sleds differed, but both rode on the sea floor with a forward-pointing camera mounted at an angle of 13.5 degrees down from horizontal, 0.43 m above the skids. The camera sled was towed by

attaching a 100-m polypropylene tether to a 600 kg weight at the end of the trawl cable. The tether separated the camera sled from the up-and-down motion of the ship. The weight on the trawl wire maintained an optimum low-towing angle which was necessary to keep the camera sled on the sea floor.

Photographs from level surfaces resulted in pictures of approximately 7m² of the sea floor with an area of 3m² to 4m² clear enough to quantify and identify benthic organisms. Illumination was provided by a 200-watt strobe mounted slightly above and to the side of the camera. Exposures were made every 15 seconds. At an average towing speed of 1-knot, a picture was taken at approximately eight meter intervals along the transect. Run number, time, and depth were automatically recorded on each picture frame.

The camera sled's location was calculated at touch down, lift off, and every 15 minutes during each tow. Distance of the camera sled behind the ship was calculated by triangulation using the amount of wire out as the hypotenuse and camera sled depth as one of the legs of a right triangle.

The sampling consisted of three transects starting west of the CMDA and intersecting with the lower half of the NODS. A fourth tow hung up on an outcrop shortly after commencing and had to be aborted. Data from the fourth tow are not included in this analysis.

Mean abundances of taxa from camera sled data were standardized to number of individuals per 100 m².

Trawl Analysis

A species list was compiled detailing presence of species in trawls at all three sites.

To quantify the composition of the invertebrate populations at each site, the relative abundances, mean abundances per 100 m², and number of species present were calculated for each of the six major phyla (Cnidaria, Mollusca, Annelida, Arthropoda, Echiura, Echinodermata). The phyla were then broken down into their most obvious taxonomic subgroups (e.g., echinoderms into classes, cnidarians into orders, etc.). Relative abundances, mean abundances per 100 m², and number of species were calculated for each taxonomic subgroup at each site.

To quantify species composition, the relative abundances of species from each taxonomic subgroup were calculated and compared. Species common to all sites were identified, as were species which were collected at only one site. Species similarity among the three sampling sites was calculated using the percent similarity index (sum of minimums, Krebs 1989).

To establish adequacy of sampling, cumulative species curves were generated for the three sampling sites by

plotting mean cumulative species plus or minus standard deviation determined from ten random combinations of samples (Pielou 1966).

Comparison of Farallon 1991 Trawl Data and Camera Sled Data

Eleven of the 13 successful trawls taken at the Farallon site in 1991 followed segments of camera sled tracks closely enough to be comparable. Data from these 11 trawls and comparable camera sled segments were used to quantify differences between trawl and camera sled methodologies in determining invertebrate composition at the Farallon site. Relative abundances and mean abundances per 100 m² were calculated from trawls and camera sled photographs for each of the five major phyla: Cnidaria, Mollusca, Arthropoda, Echiura, Echinodermata (annelids were excluded because they were generally not seen in camera sled photographs). A percent similarity index of taxa between the two sampling methods was calculated (sum of minimums, Krebs 1989). The two dominant phyla were then divided into taxonomic subgroups (e.g., echinoderms into classes, cnidarians into orders). Mean abundances per 100 m² from trawls and camera sled photographs were calculated for each taxonomic subgroup. The rank order of mean abundances estimated from the two methods was tested by a Spearman's rank correlation.

The mean abundances of the 18 identifiable species/taxa from both the camera sled photographs and trawls were compared using Spearman's rank correlation and graphic analysis.

RESULTS

Overview of Trawl Data

Quantification of samples obtained from trawls is difficult. Many smaller animals may fall through the net and the net may not be continuously engaged on the bottom. The area sampled may therefore be greatly overestimated. However, the usefulness of abundance estimates increases for comparisons between samples in which the same net was used (Haedrich, Rowe, & Polloni 1975). These facts must be taken into account regarding the following trawl data, especially for mean abundances of pennatulaceans, polychaetes, ophiuroids, and bivalves.

A total of 29,400 invertebrates were collected and identified from the 29 successful trawls taken at the three sites. The numbers of organisms were distributed among the three sites as follows: At the Farallon site in 1991, 8750 individuals from 19 cnidarian species, 18 molluscan species, 20 annelid species, 10 arthropod species, 2 echiuran species, and 40 echinoderm species were collected in 13 trawls (Table 3 and Figure 4); at the Farallon site in 1992,

4404 individuals from 16 cnidarian species, 10 molluscan species, 12 annelid species, 6 arthropod species, 2 echiuran species, and 30 echinoderm species were collected in 4 trawls; at the Pioneer Canyon site 2715 individuals from 6 cnidarian species, 7 molluscan species, 34 annelid species, 7 arthropod species, 3 echiuran species, and 19 echinoderm species were collected in 4 trawls; and at the Monterey Canyon site 13,531 individuals from 10 cnidarian species, 17 molluscan species, 19 annelid species, 12 arthropod species, 3 echiuran species, and 36 echinoderm species were collected in 8 trawls .

Cumulative species curves suggest that while the Farallon site in 1991 was adequately sampled, too few trawls were taken at the Farallon site in 1992 or the Pioneer Canyon site in 1992 to adequately sample the benthic invertebrate megafauna (Figures 5 and 6). The cumulative species curve from the Farallon site in 1991 leveled off at about 12 trawls. The Monterey Canyon site was reasonably well sampled as the cumulative species curve appeared to be leveling off at 8 trawls. The Farallon 1992 and Pioneer Canyon cumulative species curves had not yet leveled off after four trawls each. It is highly unlikely that the curves would have levelled off immediately after the fourth trawl if more trawls had been taken.

At all three sites, Echinodermata was the dominant

phylum (Figure 7). Monterey Canyon had the greatest relative abundance of echinoderms with 91% of trawled invertebrates belonging to that phylum. Relative abundances of echinoderms at the Farallon site in 1991 and 1992 were similar at 76% and 78% respectively. Pioneer Canyon had the lowest relative abundance of echinoderms at 52%

At the Pioneer Canyon site 31% of trawled invertebrates were annelids (polychaetes), which is much higher than the 9% at the Farallon site in 1991, 8% at the Farallon site in 1992, and 4% at the Monterey Canyon site (Figure 7). The Pioneer Canyon site also had a higher proportion of arthropods (7%), several times greater than the 2% at the Farallon site in 1991, 1% at the Farallon site in 1992, and 1% at the Monterey Canyon site. Echiurans also comprised a larger proportion of the trawled invertebrates at the Pioneer Canyon site (6%), again several times greater than the 1% at the Farallon site in 1991, 2% at the Farallon site in 1992, and 0.4% at the Monterey Canyon site.

The relative abundances of phyla were very similar at the Farallon site in 1991 and 1992 (Figure 7). The Farallon 1991 and Farallon 1992 samples were also the most similar in terms of species composition, showing a 69% similarity (Table 4). In general, similarity of species composition decreased with increasing distance between sampling areas, possibly indicating a change in invertebrate species

composition and abundance with distance along the central California coast. The exception was the Pioneer Canyon and Monterey Canyon sites (a distance of 88 km) which had a species similarity of only 33%. Trawls taken at the Farallon site in 1991 and 1992 had a species similarity of 44% and 46% respectively with the Pioneer Canyon site (a distance of 56 km) and 39% and 42% with the Monterey Canyon site (a distance of 145 km).

It is also possible that differences in species similarity among sites reflects differences in depths covered by trawls at each of the sites (Tables 1 and 2). This may be especially true for species similarities between Pioneer Canyon and the other sites. Trawls taken in Pioneer Canyon were deeper than all trawls at the Farallon site in 1991 and 1992 and only overlapped in depth with two of eight of the Monterey Canyon trawls.

The species similarity of only 69% between the Farallon 1991 and 1992 trawls may indicate some seasonal change or may reflect differences in depths covered (Tables 1 and 2). However, 13 trawls were taken in 1991 and only 4 were taken in 1992. It is possible that the greater number of trawls in 1991 were simply collecting more rare animals and therefore skewing the percent similarity. To examine this, the 25 most abundant species from 1991 were determined. These species represented 90% of the total invertebrates

collected at the Farallon site in 1991. As these are common species, they should be collected in fairly similar quantities in fewer trawls. A percent similarity analysis of these species was done between the Farallon 1991 and Farallon 1992 site resulting in a 66% similarity, 3% lower than the total species percent similarity between the two sites (Tables 4 and 5). Some minor seasonal variation at this site is therefore a possibility.

The mean abundance of all invertebrates was greatest at the Monterey Canyon site with 35.27 individuals per 100 m², followed by 28.64 per 100 m² at the Farallon site in 1992, and 24.59 per 100 m² at the Pioneer Canyon site (Figure 8). The Farallon site in 1991 had the lowest mean abundance with 17.85 individuals per 100 m². At all three trawling sites the mean abundance of echinoderms per 100 m² was considerably higher when compared to the other phyla. Monterey Canyon had the highest echinoderm mean abundance with 31.8 individuals per 100 m², followed by the Farallon site in 1992 with 22.4 individuals per 100 m², the Farallon site in 1991 with 13.4 per 100 m², and Pioneer Canyon with 11.8 per 100 m².

The mean abundance of cnidarians per 100 m² was relatively low at all three sites. The Farallon site in 1991 had the highest mean abundance of cnidarians with 1.8 individuals per 100m², second only to echinoderms. At the

Farallon site in 1992 and the Pioneer Canyon and Monterey Canyon sites, Cnidaria was the third most abundant phylum with mean abundances of 1.7 individuals per 100 m², 0.3 per 100 m², and 0.4 per 100 m² respectively.

The mean abundance of annelids (polychaetes) per 100 m² was fairly high at the Pioneer Canyon site with 8.7 individuals per 100 m², second only to echinoderms. At the Farallon site in 1992 and the Monterey Canyon site, polychaete mean abundances were 2.7 individuals per 100 m² and 1.6 per 100 m² respectively, also second to echinoderms but at much lower abundances than at the Pioneer Canyon site. Polychaete mean abundance at the Farallon site in 1991 was third after echinoderms and cnidarians at 1.5 individuals per 100 m².

The mean abundance of molluscs collected at the Farallon site in 1991, the Farallon site in 1992, Pioneer Canyon, and Monterey Canyon was uniformly low at 0.6 individuals per 100 m², 0.8 per 100 m², 0.6 per 100 m², and 0.7 per 100 m² respectively.

The mean abundance of arthropods was also low at the Farallon site in 1991 and 1992 and at the Monterey Canyon site with 0.3 individuals per 100 m², 0.4 per 100 m², and 0.5 per 100 m² respectively. At the Pioneer Canyon site the mean abundance of arthropods was also fairly low at 1.5 individuals per 100 m², but this was three to five times

higher than at the other three sites. Similarly, the mean abundance of echiurans was uniformly low at the Farallon site in 1991 and 1992, and the Monterey Canyon site with 0.2 individuals per 100 m², 0.7 per 100 m², and 0.2 per 100 m² respectively. Again, at the Pioneer Canyon site the mean abundance of echiurans, while also fairly low at 1.7 individuals per 100 m², was several times higher than at the other three sites.

Cnidaria

At the Farallon site in 1991, 910 cnidarians were collected representing 12 anemone species (corallimorpharians and actiniarians combined), 5 sea pen species, and 1 scleractinian species (true coral) (Figure 9). One unidentified gorgonacean (sea fan or sea whip) was also collected at this site. At the Farallon site in 1992, 314 cnidarians were collected representing 9 anemone species, 3 sea pen species, 1 alcyonacean species, and 1 scleractinian species. Some as yet unidentified gorgonaceans and antipatharians were also collected. At the Pioneer Canyon site only 12 cnidarians were collected, including 3 anemone species, 2 sea pen species, and 1 unidentified gorgonian species. At the Monterey Canyon site 157 cnidarians were collected that included 6 anemone species and 2 sea pen species. One unidentified gorgonacean and one unidentified

antipatharian were also collected at the Monterey Canyon site. Specimens from the orders Gorgonacea and Antipatharia have not yet been identified from any of the sampling sites. Three cnidarian species were collected at all three sites (Table 6). Ten cnidarian species were found at only one site (Table 7).

Corallimorphus spp. was the most abundant anemone collected at the Farallon 1991 and 1992 site and the Monterey Canyon site with 503, 63, and 63 individuals respectively (Figures 10 a and b). These specimens probably consist of more than one species of Corallimorphus, and possibly a new species; no species of Corallimorphus has been reported previously from the north Pacific (Daphne Fautin, personal communication). Paraphelliactis pabista was the most abundant anemone at the Pioneer Canyon site with four specimens. However, only six anemones were collected at Pioneer Canyon.

The mean abundance of anemones was low at all three sampling sites, ranging from a mean high of 1.1 per 100 m² at the Farallon site in 1991 to a mean low of 0.04 per 100 m² at the Pioneer Canyon site (Figure 11).

Two species of the genus Kophobelemnnon were the most abundant sea pens collected at all sites. Kophobelemnnon cf. stelliferum was the most abundant sea pen at the Farallon site in 1991 and 1992 and the Pioneer Canyon and Monterey

Canyon sites with 212, 173, 3, and 71 individuals respectively (Figure 12). Kophobelemnion cf. affine was the second most abundant.

The mean abundance of sea pens was low at all three sampling sites, ranging from a mean high of 1.0 per 100 m² at the Farallon site in 1992 to a mean low of 0.05 per 100 m² at the Pioneer Canyon site (Figure 11).

Mollusca

At the Farallon site in 1991, 71 molluscs were collected representing 1 polyplacophoran species, 8 gastropod species, 5 bivalve species, 1 scaphopod species, and 3 cephalopod species (Figure 13). At the Farallon site in 1992, 120 molluscs were collected including 1 polyplacophoran species, 5 gastropod species, 3 bivalve species, and 1 scaphopod species. No cephalopods were collected at the Farallon site in 1992. At the Pioneer Canyon site 15 molluscs were collected representing 3 gastropod species, 2 bivalve species, and 2 scaphopod species (one being a new species). No polyplacophorans or cephalopods were collected at the Pioneer Canyon site. At the Monterey Canyon site 291 molluscs were collected representing 1 polyplacophoran species, 5 gastropod species, 9 bivalve species, 1 scaphopod species, and 1 cephalopod species. Six molluscan species were collected at all three

sites (Table 6). Thirteen molluscan species were found at only one site (Table 7).

The most abundant gastropod species differed at all three sites (Figure 14). At the Farallon site in 1991 Lunatia pallida was most abundant with 29 individuals collected. At the Farallon site in 1992 Colus sp. A was most abundant with 14 individuals. However, these specimens were damaged and were not able to be identified to species (Henry Chaney, personal communication). Colus jordani was most abundant at the Pioneer Canyon site with four individuals. However, only ten gastropods were collected at Pioneer Canyon. At the Monterey Canyon site Steiraxis aulaca was most abundant with 60 individuals.

The mean abundance of gastropods was low at all three sampling sites, ranging from a mean high of 0.42 per 100 m² at the Farallon site in 1991 to a mean low of 0.10 per 100 m² at the Pioneer Canyon site (Figure 15). At the Farallon site in 1991 and 1992 the mean abundance of gastropods was greater than that of any of the other classes of molluscs.

At the Farallon site in 1991 and 1992 Cuspidaria glacialis was the most abundant bivalve species with 11 and 5 individuals collected respectively (Figure 16). Malletia cf. talama was the most abundant bivalve species at the Pioneer Canyon site with four individuals collected. However, only five bivalves were collected at Pioneer

Canyon. At the Monterey Canyon site Acharax johnsoni was the most abundant bivalve with 11 individuals collected.

The mean abundance of bivalves was very low at all three sampling sites, ranging from a mean high of 0.08 per 100 m² at the Monterey Canyon site to a mean low of 0.03 per 100 m² at the Pioneer Canyon site (Figure 15).

Polyplacophorans collected at the Farallon site in 1991 and 1992 and the Monterey Canyon site belonged to a single species, ?Leptochiton alveolus (Figure 17). The mean abundance of polyplacophorans at the Farallon site in 1992 was low at 0.16 per 100 m² (Figure 15), but this was many times higher than the mean abundance at the Farallon site in 1991 and the Monterey Canyon site at 0.02 and 0.01 per 100 m² respectively. No polyplacophorans were collected at the Pioneer Canyon site.

The large scaphopod species Fissidentalium megathyris was collected at all three sites (Figure 17). Fissidentalium erosum, a new species, was collected at the Pioneer Canyon site (described in Shimek & Moreno 1996). Unfortunately, the total number of Fissidentalium erosum is not known as some of them were misplaced. At the Pioneer Canyon and Monterey Canyon sites the mean abundance of scaphopods was greater than that of any of the other classes of molluscs at 0.46 and 0.45 per 100 m² respectively (Figure 15). The standard deviation of scaphopod mean abundance was

extremely high at these two sites, indicating a high degree of patchiness in the scaphopod assemblages on a scale of hundreds or even thousands of square meters. The mean abundance of scaphopods at the Farallon site in 1991 and 1992 was 0.11 and 0.26 per 100 m² respectively. The standard deviation of scaphopod mean abundance was fairly high at these two sites, also indicating patchiness, but not as high as at the Pioneer Canyon and Monterey Canyon sites.

Eight specimens representing three species of cephalopod (Benthoctopus sp., Graneledone pacifica, and Vampyroteuthis infernalis) were collected at the Farallon site in 1991 (Figure 17). Six of these were Graneledone pacifica. A single specimen of Graneledone pacifica was collected at the Monterey Canyon site. The mean abundance of cephalopods was extremely low at both sites at 0.01 and 0.003 per 100 m² respectively (Figure 15). No cephalopods were collected at the Farallon site in 1992 or the Monterey Canyon site.

Annelida (Polychaeta)

At the Farallon site in 1991, 367 polychaetes were collected representing 20 species from 12 families (Figure 18 and Table 8). At the Farallon site in 1992, 398 polychaetes were collected, representing 12 species from 9 families. At the Pioneer Canyon site 852 polychaetes were

collected, representing 34 species from 18 families. At the Monterey Canyon site 567 polychaetes were collected representing 19 species from 15 families. Six polychaete species were collected at all three sites (Table 6). Thirty-one polychaete species were found at only one site (Table 7).

Aphrodita cf. japonica, Maldane monilata, Paradiopatra sp. A, and Myriochele sp. unid. were the four most common polychaete species collected. (Figure 19). Aphrodita cf. japonica was the most abundant polychaete collected at the Farallon site in 1992 and the Monterey Canyon site with 210 and 281 individuals respectively. Paradiopatra sp. A and Maldane monilata were the second and third most abundant polychaetes at the Farallon site in 1992 and the Monterey Canyon site. At the Farallon site in 1991 Paradiopatra sp. A was the most abundant with 109 individuals collected, followed closely by Aphrodita cf. japonica and Maldane monilata respectively. Maldane monilata was the most abundant polychaete at the Pioneer Canyon site with 377 specimens. Species grouped as "other" were second-most common at Pioneer Canyon with 173 individuals representing 30 species. Myriochele sp. unid. was fairly abundant at Pioneer Canyon with 124 individuals collected. This species was not collected at the Farallon site in 1991 or 1992 and only one specimen was collected at the Monterey Canyon site.

The abundance of Aphrodita cf. japonica was relatively low at the Pioneer Canyon site compared to the other three sites, with only 17 individuals collected.

The mean abundance of polychaetes was relatively high at the Pioneer Canyon site at 8.7 individuals per 100 m², second only to echinoderm mean abundance (Figure 8). At the Farallon site in 1992 and the Monterey Canyon site the mean abundance of polychaetes was also second to echinoderm mean abundance, but at a much lower density of 2.7 and 1.6 individuals per 100 m² respectively. At the Farallon site in 1991 the mean abundance of polychaetes was third, after echinoderms and molluscs, with 1.5 individuals per 100 m². The standard deviation of polychaete mean abundance was fairly high at the Farallon site in 1991, indicating a patchy distribution. The standard deviations of polychaete mean abundances were fairly low at the other three sites, indicating a more even distribution of polychaetes.

Arthropoda

At the Farallon site in 1991, 195 arthropods were collected representing 5 pycnogonid species and 5 decapod species (Figure 20). At the Farallon site in 1992, 54 arthropods were collected representing 4 pycnogonid species and 2 decapod species. At the Pioneer Canyon site 203 arthropods were collected representing 3 pycnogonid species,

1 isopod species, and 3 decapod species. At the Monterey Canyon site 178 arthropods were collected representing 7 pycnogonid species, 1 amphipod species, 3 decapod species, and 1 cirriped species. Four arthropod species were collected at all three sites (Table 6). Eight arthropod species were found at only one site (Table 7).

At the Farallon site in 1991 and the Pioneer Canyon site Colossendeis tenera was the most abundant pycnogonid with 40 and 5 individuals collected respectively (Figure 21). However, only 10 pycnogonids were collected at Pioneer Canyon compared to 146 at the Farallon site in 1991. At the Farallon site in 1992 Pallenopsis longiseta was the most abundant pycnogonid species with 14 individuals. At the Monterey Canyon site, Colossendeis macerrima was the most abundant pycnogonid with 63 individuals, closely followed by Colossendeis tenera with 57 individuals. Colossendeis peloria, a new species, was collected at the Monterey Canyon site (described in Child 1994).

At the Farallon site in 1991 the anomuran crab Paralomis verrilli was the most abundant crustacean with 23 individuals collected (Figure 22). At the Farallon site in 1992 only two crustacea species were collected. Cranxon abyssorum was the most abundant crustacean with 18 individuals collected, followed by Munidopsis verrilli with 5 individuals collected. At the Pioneer Canyon site the

isopod Storothyngura bicornis accounted for 184 of the 192 crustaceans collected. At the Monterey Canyon site the dominant crustacean was the barnacle Gymnoscalpellum sp. with 12 specimens collected.

The mean abundance of arthropods was extremely low at all three sampling sites, generally .20 per 100 m² or lower for all taxonomic subgroups (Figure 23). There were two exceptions to this: At the Pioneer Canyon site the mean abundance of the isopod Storothyngura bicornis was 1.28 per 100 m² with an extremely high standard deviation of 1.6, indicating a high degree of patchiness. At the Monterey Canyon site the mean abundance of pycnogonids was .40 per 100 m², several times greater than the mean abundances of all the other crustaceans groups at all sites except for S. bicornis at the Pioneer Canyon site.

Echiura

Ninety-six echiurans were collected at the Farallon site in 1991, 103 at the Farallon site in 1992, 165 at the Pioneer Canyon site, and 60 at the Monterey Canyon site (Figure 24). The phylum echiura had the fewest number of trawled species of any of the six major invertebrate phyla. Alomasoma nordpacificum and Choanostomellia bruuni were the only identified echiuran species and were collected at all three sites. Alomasoma nordpacificum was the most abundant

echiuran collected at all three sites with 93, 83, 153, and 41 individuals respectively. Unidentified echiurans, probably all of one species, were collected at the Pioneer Canyon and Monterey Canyon sites. These echiurans could not be identified because of damage they sustained in the trawls.

The mean abundance of echiurans was highest at the Pioneer Canyon site at 1.71 individuals per 100 m² (Figure 8). At the other three sites the mean abundance of echiurans was less than 1.0 per 100 m².

Echinodermata

At the Farallon site in 1991, 6779 echinoderms were collected representing 15 asteroid species, 10 ophiuroid species, 3 echinoid species, and 12 holothurian species (Figure 25). No crinoids were collected at the Farallon site in 1991. At the Farallon site in 1992, 3430 echinoderms were collected representing 7 asteroid species, 10 ophiuroid species, 2 echinoid species, 10 holothurian species, and 1 unidentified crinoid species. At the Pioneer Canyon site 1405 echinoderms were collected representing 4 asteroid species, 7 ophiuroid species, 2 echinoid species, and 6 holothurian species. No crinoids were collected at the Pioneer Canyon site. At the Monterey Canyon site 12,281 echinoderms were collected representing 11 asteroid species,

9 ophiuroid species, 2 echinoid species, 13 holothurian species, and 1 unidentified crinoid species. Crinoids from the Farallon site in 1992 and the Monterey Canyon site could not be identified because of damage sustained during trawling. Sixteen echinoderm species were collected at all three sites (Table 6). Eighteen echinoderm species were found at only one site (Table 7).

Eremicaster pacificus was by far the most abundant asteroid collected at all three sites with 481, 230, 231, and 338 individuals respectively (Figures 26 and 27). The relative abundances of the remaining asteroid species were relatively low at all sites, with the exception of Benthopecten acanthonotus at the Monterey Canyon site with 240 specimens collected.

The mean abundance of asteroids was fairly consistent at all three sampling sites, ranging from a mean high of 1.8 per 100 m² at the Pioneer Canyon site to a mean low of 1.3 per 100 m² at the Farallon site in 1991 (Figure 28).

Amphiura carchara was the most abundant ophiuroid collected at the Farallon site in 1991 and 1992 and at the Pioneer Canyon site with 764, 525, and 282 individuals respectively (Figure 29 - originally published in Summers 1993). Amphilepis platytata was the most abundant ophiuroid at the Monterey Canyon site with 964 specimens collected. A. platytata was the second most abundant ophiuroid at the

other sites.

The mean abundance of ophiuroids was relatively high at all three sampling sites, ranging from a mean high of 8.2 per 100 m² at the Monterey Canyon site to a mean low of 3.1 per 100 m² at the Farallon site in 1991 (Figure 28). The standard deviation of ophiuroid mean abundance was extremely low at the Monterey Canyon site, indicating a uniform distribution.

Tromikosoma panamense was the most abundant echinoid at the Farallon site in 1991 and the Pioneer Canyon and Monterey Canyon sites with 83, 7, and 45 individuals respectively (Figure 30). At the Farallon site in 1992 Aeropsis fulva was the most abundant echinoid with 18 specimens. Urechinus sp. was only collected at the Farallon site in 1991 and could not be identified to species because the fragile tests were greatly damaged in the trawls (Richard Mooi, personal communication).

The mean abundance of echinoids was consistently very low at all three sampling sites, ranging from a mean high of .18 per 100 m² at the Farallon site in 1992 to a mean low of .09 per 100 m² at the Pioneer Canyon site (Figure 28).

The holothurians Echinocucumis hispida and Ypsilothuria bitentaculata of the family Ypsilothuridae were the most abundant holothurians at the Farallon site in 1991 and 1992 and at the Pioneer Canyon site with 2587, 1661, and 309

individuals respectively (Figures 31 and 32). These two species cannot be told apart without dissecting out the skin ossicles and so were combined under Ypsilothuridae. At the Farallon site in 1991 Paelopadites confundens was the second most abundant holothurian with 1038 specimens. At the Farallon site in 1992 Molpadia intermedia was the second most abundant holothurian with 227 specimens. At the Pioneer Canyon site Molpadia musculus was second in abundance with 214 specimens. At the Monterey Canyon site Scotoplanes globosa was the most abundant holothurian with 4602 individuals collected. Ypsilothuridae were second in relative abundance at the Monterey Canyon site with 1453 individuals.

A new species of the holothurian genus Anapta was collected at the Farallon site in 1992. To date this species has not been named or further described.

The mean abundance of holothurians was higher at all three sampling sites than that of any other invertebrate group, ranging from a high of 21.8 individuals per 100 m² at the Monterey Canyon site to a low of 6.4 per 100 m² at the Pioneer Canyon site (Figure 28).

Farallon 1991 Trawls versus Comparable Camera Sled Segments

A total of 5014 invertebrates were collected in 11 trawls compared to 26192 counted in comparable camera sled

photographs (Figure 33). Echinoderms were the dominant phylum in trawls with a relative abundance of 82%, followed by cnidarians at 13%. The opposite was true in the camera sled photographs where cnidarians accounted for 70% of invertebrates, followed by echinoderms at 26%.

The relative abundances of the remaining three identifiable phyla were fairly similar between the trawls and camera sled. The relative abundance of molluscs was 1% in trawls and 0.1% in the camera sled photographs (Figure 33). The relative abundance of arthropods was 3% in trawls and 2% in the camera sled photographs. The relative abundance of echinurans was 2% in the trawls and 1% in the camera sled photographs.

A percent similarity analysis performed on the abundance of taxa between trawls and comparable camera sled segments was fairly low at 40%, suggesting disparity between the two sampling methods (Table 4).

The mean abundance of taxa per 100 m² estimated from the trawls was always less than that in camera sled photographs (Table 9). The total mean abundance of invertebrates was 322.17 per 100 m² in the camera sled photographs and 10.22 per 100 m² in the trawls.

Echinoderms and cnidarians, the two dominant phyla in both trawls and comparable camera sled segments, were broken down into classes and orders respectively and analyzed. The

mean abundance of anemones was 0.65 per 100 m² in trawls and 17.45 per 100 m² in the camera sled photographs (Figure 34). The mean abundance of sea pens was extremely disparate between the two methods with 0.5 individuals per 100 m² collected in trawls and 209 individuals per 100 m² seen in camera sled photographs.

The mean abundance of asteroids was fairly low for both sampling methods with 0.9 individuals per 100 m² in trawls and 1.1 per 100 m² in camera sled photographs. The same is true for echinoids with a mean abundance of 0.13 per 100 m² in trawls and 0.39 per 100 m² in camera sled photographs (Figure 35). The mean abundance of ophiuroids was very low in trawls at 2.2 per 100 m² when compared to 69 per 100 m² seen in camera sled photographs (Figure 35). The mean abundance of holothurians was fairly high in trawls at 5.3 per 100 m². However, the mean abundance of holothurians was almost three times greater in camera sled photographs at 14 per 100 m² (Figure 35).

The mean abundance of molluscs was very low in trawls and camera sled photographs with 0.11 and 0.36 individuals per 100 m² respectively (Figure 36). The mean abundance of arthropods in trawls was very low at 0.24 individuals per 100 m² when compared to 5.4 per 100 m² in camera sled photographs. The same is true for echiurans with a mean abundance of 0.19 per 100 m² in trawls and 5.1 per 100 m² in

camera sled photographs.

Analysis of the rank order of abundances of the above taxa by a Spearman's rank correlation test gave an $r_s = .63$ ($0.05 < p < 0.10$), suggesting that the two sampling methods surveyed different populations (Table 9). Considering that many of the ranks were either tied (molluscs, ophiuroids, echinoids) or similar (anemones, arthropods, echiurans), it appears that pennatulaceans, asteroids, and holothurians accounted for the lack of statistical correlation.

Eighteen taxa were found to be both adequately sampled by trawls and visible and identifiable in camera sled photographs (Figure 37). The mean abundances of these 18 taxa were always greater in camera sled photographs than in trawls, except for the asteroid Benthopecten acanthonotus. The standard deviations of the mean abundances of Corallimorphus spp., Pannychia mosleyi, Paelopadites confundens, Asteronyx loveni, and Ophiomusium glabrum were extremely high in camera sled data, indicating a high degree of patchiness for these species or relatively narrow depth preferences.

Analysis of the rank order of abundances of the above identifiable taxa by a Spearman's rank correlation test gave an $r_s = .45$ ($0.05 < p < 0.10$), suggesting that the two sampling techniques surveyed different populations (Table 10). However, the first four rankings were of comparable species,

indicating that the most common identifiable species were sampled similarly by both methods, although at much lower mean abundances in trawls.

DISCUSSION

Local Zoogeographic Distribution:

Changes in species composition and abundance of benthic invertebrate megafauna correlated with distance along the central California coast. In general, the greatest changes occurred with increasing distance between sites (Table 4). The Farallon site samplings in 1991 and 1992 were, as expected, most similar to each other (69% for all species; 66% for the 25 most common species). Pioneer Canyon, the closest site to the Farallon 1991/1992 site, showed the next highest similarity (44% and 46% respectively). Monterey Canyon, the site furthest from the Farallon 1991/1992 site, showed the least similarity to those sites (39% and 42% respectively). However, the Farallon site in 1991 and 1992 showed a higher percent similarity to the Monterey Canyon site than did the Pioneer Canyon site (33%), which was 56 km closer. However, Pioneer Canyon may not have been adequately sampled (Figure 6). If more trawls had been taken at Pioneer Canyon, the similarity to Monterey Canyon may have changed.

At all three sites Echinodermata was the dominant

phylum. The relative abundances of echinoderms at the Farallon site in 1991 and 1992 were very similar (76% and 78% respectively), followed by Cnidaria (10% and 7% respectively) (Figure 7). However, echinoderms accounted for only 52% of trawled invertebrates at the Pioneer Canyon site, but the annelids (polychaetes) were second at 31%. Cnidarians were virtually non-existent in the Pioneer Canyon trawls, accounting for less than 1% of all individuals.

Although only four trawls were taken at the Pioneer Canyon site, many more individual polychaetes and almost twice as many species of polychaetes were collected at this site than at any other site (Figures 18 and 19). Also, the relative abundances of echiurans and arthropods were several times greater at the Pioneer Canyon site than at the other sites (Figure 7). The significance of this high relative abundance of arthropods is nullified when it is realized that 90% of the arthropod individuals were represented by a single species, the isopod Storthyngura bicornis. The abundances of the remaining arthropod species were quite low (Figures 21 and 22). The Pioneer Canyon site is qualitatively different from the other sites with high numbers of polychaetes and echiurans, reduced numbers of holothurians, and a virtual absence of cnidarians. In contrast, at the Monterey Canyon site a prodigious 91% of all trawled invertebrates were echinoderms, of which

approximately 60% were holothurians and 25% were ophiuroids (Figures 7, 29, and 32). The remaining five phyla accounted for only 9% of the total invertebrates collected in Monterey Canyon.

Differences in the relative abundances of the six invertebrate phyla at these sites are undoubtedly due to a number of factors, including upwelling, depositional differences, and currents. One of the major upwelling areas off the coast of California is found near Monterey Canyon (Breaker & Broenkow 1989). The effects of this upwelling probably contribute to greater sediment and organic accumulation in the Canyon. This in turn creates ideal nutrient conditions for sediment feeding elasipodid holothurians, such as Elpidia cf. theeli and Peniagone cf. incerta (Billett et al. 1984; Pawson & Foell 1986; Miller & Pawson 1990; David Pawson, personal communication), which were only found at the Monterey Canyon site (Figure 32). Ophiuroid abundances may also be influenced by nutrient availability (Summers 1993). Of the three sites, the Monterey Canyon had the highest mean abundance of ophiuroids (Figure 28).

The incorporation of phytodetritus into deep-sea sediment is another important factor affecting faunal abundances (Smith, C.R. 1994; Smith et al. 1994). In July 1990 massive amounts of phytodetritus were observed in

Monterey Canyon at depths greater than 3000 m, much greater than anything seen in camera sled photographs from the Farallon site in July 1991 (Barbara Hecker, personal communication). This massive influx of material containing large amounts of organic matter may explain why Monterey Canyon had the highest total mean abundance of invertebrates per 100 m² of all three sites (Figure 8).

Certain species of holothurians, such as Scotoplanes globosa, aggregate where large concentrations of phytodetritus accumulate (Ohta 1983; Billett 1991). Two trawls taken at the Monterey Canyon site in 1992 contained a total of 4,602 specimens of the elasipodid holothurian Scotoplanes globosa (Figure 32). The same two trawls contained 869 specimens of Peniagone cf. incerta and 374 specimens of Elpidia sp. cf. theeli. None of these species were collected in any of the other six trawls taken at the Monterey Canyon site. These species may be aggregating in an area of an abundant food source provided by upwelling or deposition of phytodetritus.

The deep-sea benthic community can be quite variable, even within a relatively small area (Lauerman et al. 1996). It is interesting that although 3160 ophiuroids were collected at the Monterey Canyon site (Figure 29), not a single ophiuroid was collected in the two trawls in which high numbers of Scotoplanes globosa, Peniagone cf. incerta,

and Elpidia sp. cf. theeli. were collected. Many deep-sea ophiuroids appear to feed on detritus in the sediment or on small epi- or infaunal organisms (Tyler 1980; Pearson & Gage 1984; Gage & Tyler 1991). The absence of ophiuroids in these two trawls may be due to competition or disturbance from these three species of elasipodid holothurians. This result illustrates the need to adequately survey large areas of the deep sea to describe megafaunal community structure.

Thurston et al. (1994) reported that a strong seasonal pulse of phytodetritus to the sea floor resulted in abundant surface-grazing holothurians and high biomass values. However, in geographically close areas that lack this input of phytodetritus they reported no large invertebrates and biomass values 16-39 times lower than at the previous site. While the Monterey Canyon site was dominated by large epifaunal holothurians, Pioneer Canyon had a single specimen of epifaunal holothurian (Scotoplanes globosa). The remainder of the holothurians were infaunal (Figure 32). However, polychaetes and echiurans were extremely abundant at the Pioneer Canyon site compared to the Monterey Canyon and Farallon site (Figure 8). The Pioneer Canyon site may have a limited input of phytodetritus resulting in fewer large epifaunal invertebrates and greater numbers of smaller animals which can survive with reduced food input.

A notable difference among the three sites was the

relatively high mean abundance of cnidarians at the Farallon site in 1991 and 1992 compared to the low mean abundance of cnidarians at the Monterey Canyon site and the virtual absence of cnidarians at the Pioneer Canyon site (Figure 8). Sea pens and anemones are filter feeders and can be common in areas of moderately high-energy bottoms in the deep sea; sea pens actively orient to the changing direction of bottom currents and are more common where organic matter is suspended into the water column by bottom currents (Gage & Tyler 1991; Gary Williams, personal communication). The high abundances of sea pens and anemones collected in trawls and seen in camera sled photographs at the Farallon site indicate that this is an area with active bottom currents which results in the suspension of organic material in the water column.

Aller (1997) found that under low-flow conditions at a deep-sea site the total number of epifauna decreased, abundances of infaunal animals and tube builders increased, and a higher proportion of smaller individuals were found. These characteristics are strongly descriptive of the invertebrate fauna collected at Pioneer Canyon site. The virtual absence of cnidarians from this site may be due to the presence of low velocity currents.

The reduced number of cnidarians in Monterey Canyon compared to the Farallon site may also be due to low-

velocity currents. Elapodid holothurians may be more abundant in areas of reduced flow conditions (Billett 1991). However, these holothurians were only present in two of eight trawls in Monterey Canyon. Large numbers of ophiuroids were present in the remaining six trawls, however, at higher mean abundances than at the Farallon site in 1991 or 1992 (Figure 28). The large numbers of ophiuroids may create an element of disturbance that is reducing the number of cnidarians in Monterey Canyon.

It is likely that a number of interacting factors account for the zoogeographic differences seen in this study.

Seasonality

Traditionally, deep-sea benthic ecosystems were thought to exhibit great constancy because of very stable physical factors such as salinity, temperature, and oxygen. However, many recent studies have demonstrated that seasonal fluctuations in the deposition of phytodetritus greatly affect spatial and temporal patchiness in the deep-sea (Lampitt 1985; Alldredge & Silver 1988; Thiel et al. 1988; Tyler 1988). Seasonal blooms in surface waters bring a downward pulse of particulate matter from the euphotic zone. Gage and Tyler (1991) estimated that 1-3% of surface primary production reaches the deep sea. In temperate latitudes

considerable accumulation occurs soon after the spring bloom and continues into summer. This seasonal influx is an important periodic food source for deep-sea benthic communities (Billett et al. 1983; Hecker 1990b). Certain species, such as the echinoid Echinus affinus, actively show a preference for areas of the sea floor that are covered with phytodetritus, while other species, such as the holothurian Benthogone rosea, seem oblivious to this detrital carpet (Lampitt 1985). Additionally, resuspension of this detritus by bottom currents is thought to be beneficial to suspension feeders, such as sea pens and anemones (Lampitt 1985).

Trawl data from the Farallon site indicate some seasonal variability in species composition at this site. Percent similarity between the Farallon site in 1991 (summer) and the Farallon site in 1992 (winter), while greater than among any other sites, was only 69% for all species (Table 4). However, only four successful trawls were taken at this site in 1992, whereas 13 successful trawls were taken in 1991. The cumulative species curve for 1992 had not leveled off by four trawls (Figure 5). Therefore it seems reasonable that more rare species were caught in 1991, and indeed a greater number of species per phylum, except echiura, were found in 1991 compared to 1992 (Figure 4).

Given that a greater number of trawls collected more rare species, it seemed reasonable that the most common 25 species collected in 1991 would be similarly represented in 1992 if seasonality was not a factor. However, there was only a 66% similarity between the two sites for these 25 species (Table 5). While the relative abundances of the six major phyla were fairly similar between the two sites (Figure 7), there were some major differences in species composition.

Holothurians remained the dominant group at this site, but species composition was seasonally different. Paelopadites confundens was present in large numbers (1038) in 1991 but was barely present (10) in 1992 (Figure 31). However, this species is benthopelagic and has been found swimming at 500-1000 meters above the sea bed, indicating an ability to move long distances (Miller & Pawson 1990). Benthopelagic holothurians often have a patchy distribution which may vary temporally and spatially; this distribution is possibly related to an opportunistic lifestyle (reviewed in Billett 1991). Thus in the summer of 1991 when the downward flux of phytodetritus from the spring bloom to the sea floor may have been at its peak, Paelopadites confundens may have been present in greater numbers on the sea floor to feed on this detritus, leading to a greater number caught in summer trawls.

The holothurian Pannychia moseleyi was not found at all at the Farallon site in 1992 (Figure 31). However, the reported depth range for this species in the central Eastern Pacific is 212 to 2599 meters (Maluf 1988) and off the Oregon Coast it has been found from 700 to 2400 meters (Carney & Carey 1976). At the Farallon site in 1991 Pannychia moseleyi was found only in the two most shallow trawls, between 2300 and 2570 meters. At the Farallon site in 1992 all trawls were taken between 2850 and 3000 meters, below the known depth range of this species.

Certain holothurian species showed little change in relative abundance between the summer of 1991 and winter of 1992. The family Ypsilothuridae remained dominant at both sampling times. The relative abundances of Molpadia spp. and Protankyra abyssicola were also similar. However, these species are infaunal and they are nonmotile due to highly reduced or absent tube feet. Therefore a seasonal difference in their abundance would be highly unlikely.

Pennatula phosphorea was collected in relatively abundant numbers (64) in 9 of 13 trawls at the Farallon site in the summer of 1991, at depths ranging from 2300 to 3075 m. However, P. phosphorea was not collected in any of the four trawls taken at the Farallon site in the winter of 1992 (Figure 12). Although little is known of the life histories of deep-sea sea pens, it is likely that they are long-lived

and growth is probably relatively slow (Gary Williams and Gilbert Van Dykhuizen, personal communication). It is therefore doubtful that there is a seasonal component to the absence of this species in the 1992 trawls. In camera sled photographs from the summer of 1991, Pennatula phosphorea accounted for 29% of the total megafauna and was the most abundant identifiable species seen in the entire survey. However, its distribution was quite patchy and its distribution appeared to be controlled by topography and sea-floor stability rather than depth (Hecker 1992). It is therefore likely that patchiness accounts for its absence in the 1992 trawls, rather than any seasonal component.

The asteroid Psilaster pectinatus was relatively abundant (70) in the trawls at the Farallon site in 1991. However, Psilaster pectinatus was not collected at all in the Farallon 1992 trawls (Figure 26). In the Farallon 1991 trawls, Psilaster pectinatus was only found in trawls from shallower depths ranging from 2300 to 2570 meters. These trawls did not contain the usually very abundant asteroid Eremicaster pacificus. In the Farallon 1992 trawls all four trawls were deeper, between 2850 and 3000 meters, and each contained high numbers of Eremicaster pacificus and no Psilaster pectinatus. Although Psilaster pectinatus has a reported depth range of 1500 to 3000 meters (Alton 1966), it seems to occupy a much less extensive range off the

Farallones. Both species are sediment ingestors; therefore, competition rather than seasonality may explain why both were not present in similar trawls at similar depths.

The large ophiuroid Ophiomusium glabrum was collected in high numbers (160) in trawls at the Farallon site in 1991 but was not present in the Farallon 1992 trawls (Figure 29). Seasonal reproductive patterns in deep sea ophiuroids may be linked to seasonal changes in the downward flux of organic matter from the surface (Tyler 1986). However, it is not known if O. glabrum shows any distinct seasonal variation in reproduction or population structure which would account for its absence in 1992. Given its large size, O. glabrum is probably relatively long-lived. Therefore its absence at the Farallon site in 1992 is probably not due to recruitment (Gordon Hendler, personal communication). In camera sled photographs, O. glabrum was common between 2500 and 2800 m and rare below 2800 m. (Hecker 1992). At the Farallon site in 1991, O. glabrum was found only in the three most shallow trawls between 2300 and 2760 m. At the Farallon site in 1992 all trawls were taken between 2850 and 3000 meters, below the common depth range of this species.

Certain species were collected in substantial numbers in the 4 trawls at the Farallon site in 1992 which were not collected at all in the 13 trawls at the Farallon site in 1991. These include the holothurian Psolidium gracile

(Figure 31), the pycnogonid Pallenopsis longiseta (Figure 21), and the ophiuroid Ophiacantha eurypoma (Figure 29). This implies a seasonal variation in abundance of these three species at the Farallon site. Unfortunately, there is virtually no information in the literature regarding Psolidium or Ophiacantha. Pallenopsis longiseta, with a known depth range from 1228 to 4100 meters, is a mobile species which is possibly quite common in deep slopes and basins of the Pacific Ocean. However, none have been taken in similar depths off the Oregon coast after years of sampling (Child 1994). Its depth distribution remains unknown and there is no information available regarding reproduction in this species. The reason for the absence of Pallenopsis in the Farallon 1991 trawls and its subsequent presence in the Farallon 1992 trawls remains unknown.

Although there appear to be some seasonal differences in the abundance of certain invertebrate megafaunal species at the Farallon site, competition, patchiness, and depth of trawls appear to be responsible for a number of the differences seen in species abundance.

Comparison of Sampling Methods: Trawls versus Camera Sled

There are a number of biases inherent in the use of trawls: Many fragile and/or small invertebrates such as pennatulaceans, polychaetes, and certain gastropods, bivalves, scaphopods, and ophiuroids may fall through the

net or be destroyed during the trawl; the actual time the net spends engaged on the bottom is uncertain and therefore the efficiency of trawls, in terms of numbers of animals captured versus the actual number in the area sampled, is generally quite low. Trawls are therefore semi-quantitative at best and underestimate absolute abundance (reviewed in Haedrich, Rowe, & Polloni 1975; Eleftheriou & Holme 1984). The mean abundances of taxa reported in this thesis are to be considered minimal. However, these mean abundances have value in that they may be used in comparison to the mean abundances obtained by the camera sled.

For many invertebrate megafaunal taxa there is a great disparity in results of trawl sampling versus camera sled sampling, with trawls tending to underestimate the actual abundance of many species (Uzmann et al. 1977). This was evidenced in this study by only a 40% similarity in taxa between the two methods (Table 4) and was especially true for cnidaria and echinodermata. Cnidarian abundances are often severely underestimated in trawls compared to camera sled abundances. Studies using trawls on the continental slope south of New England (Haedrich, Rowe, & Pollini 1980) did not report a cerianthid anemone or the sea pen Distichoptilum gracile commonly seen in camera sled photographs taken in the same vicinity (Hecker 1990a). This disparity holds true for this study and was particularly

true for pennatulaceans as the mean abundance of pennatulaceans per 100 m² was over 400 times greater in camera sled photographs than in trawls (Figure 34). Many small, fragile pennatulaceans are either falling through the net, being destroyed during the trawling process, or are not sampled reliably by the trawl because they are attached firmly to the sea floor and extend only slightly above the sediment.

The difference in anemone abundances between the two sampling methods was less dramatic but still substantial, with 25-times-greater anemone mean abundances in camera sled photographs than in trawls. This was true even for the relatively large and sturdy corallimorpharians of the genus Corallimorphus, which had a mean abundance 12 times higher in camera sled photographs than in trawls (Figure 37 and Table 10). Corallimorphus spp. are too large to fall through the net and are not fragile enough to be easily destroyed during the trawling process. It therefore also seems probable that the net is not engaged on the sea floor continuously and that therefore the area trawled is greatly overestimated, or that the trawl is not reliably sampling anemones which are securely fixed to the sea floor. For Cnidaria, at least, trawls appear to be woefully inadequate in giving a realistic assessment of mean abundances.

A comparison of echinoderm mean abundances also shows a

great disparity between trawls and camera sled results. Although holothurians were the dominant echinoderm in trawls in terms of relative and mean abundances, the mean abundance of holothurians in camera sled photographs was almost three times greater than in trawls (Table 9 and Figure 35).

Pannychia moseleyi, Benthodytes sanguinolenta, and Paelopadites confundens are three epifaunal holothurian species that are relatively large and would not fall through the net. The mean abundances of these three species were consistently higher in camera sled photographs than in trawls (Figure 37 and Table 10).

A comparison of overall ophiuroid mean abundance also shows a great disparity between the two sampling methods with over 30 times more ophiuroids seen in camera sled photographs than collected in trawls (Figure 35 and Table 9). Members of the families Amphiuridae and Amphilepididae are primarily infaunal (Gage & Tyler 1991) but they extend their arms above the surface and therefore were counted in camera sled photographs, even though individuals could not be identified to species. As ophiuroids are usually small, fragile animals, they are often mangled in trawls or may fall through the net. Thus an underestimation of their mean abundance is to be expected.

Ophiomusium glabrum was the largest ophiuroid collected in trawls in this study with a disc diameter of up to 40 mm

(Summers 1993). This species was large enough to be identified in camera sled photographs and had a mean abundance over five times greater than in trawls (Figure 37 and Table 10). This large, relatively sturdy species is not as likely to fall through the net. The low mean abundance of Ophiomusium in trawls again suggests that the net is not continuously engaged on the sea floor.

The camera sled sampled three times as many echinoids as did trawls (Figure 35 and Table 9). This was true even though the irregular burrowing urchin, Urechinus sp., was collected in trawls but was not recorded by the camera sled. Tromikosoma panamense was identified in camera sled photographs with a mean abundance approximately five times greater than when collected in trawls (Figure 37 and Table 10). Since this is a very large, sturdy urchin which would not fall through the net nor be destroyed during the trawling process, these results again suggest that the net is not continuously engaged on the sea floor.

Asteroidea is the only class of echinodermata in which the mean abundances were fairly similar between the two sampling methods, with camera sled abundances only slightly higher than trawl abundances (Figure 35 and Table 9). Four asteroid families and one asteroid species were identified in camera sled photographs and collected in trawls: Zoroasteridae, Pterasteridae, Goniasteridae, Solasteridae,

and Benthopecten acanthonotus. The mean abundances of each of these families was higher in camera sled photographs than in trawls (Figure 37 and Table 10). However, the mean abundance of Benthopecten acanthonotus was greater in trawls than in camera sled photographs, the only species/taxon for which this was true. One explanation for this is that Benthopecten acanthonotus lives semi-buried in the sediment (Barbara Hecker, personal communication) and for this reason may not be always visible in camera sled photographs.

A comparison of molluscan mean abundances continues the disparity between the two sampling methods. The camera sled sampled over three times as many molluscs as did trawls (Figure 36 and Table 9). However, both methods are probably severely underestimating molluscan abundances. Trawls probably are not always engaged on the sea floor and small scaphopods, bivalves, and gastropods may fall through the net. Bivalves and scaphopods are infaunal and are rarely seen in camera sled photographs. Benthic octopods can easily avoid the trawl net or the oncoming camera sled. Gastropods are seen in camera sled photographs but are relatively small and often sediment-colored and may be easily overlooked. With respect to molluscs, trawls did have several advantages over the camera sled in that a number of bivalves, many specimens of the scaphopod Fissidentalium megathyris, as well as specimens of

Leptochiton alveolus were collected. No chitons, scaphopods, or bivalves were seen in comparable camera sled photographs.

A comparison of arthropod and echiuran mean abundances also indicates a great disparity between trawls and camera sled results. For both phyla, over 20 times more individuals were seen in camera sled photographs than were collected in trawls (Figure 36 and Table 9).

With respect to Arthropoda, the camera sled was only effective in sampling the larger crabs, shrimp, and pycnogonids, and produced much higher mean abundances than trawls. For example, the mean abundances of the anomuran crabs Paralomis verrilli and Munidopsis verrilli were approximately 4 times and 50 times higher respectively in camera sled photographs than in trawls (Figure 37 and Table 10).

Echiurans are burrowers and can only be seen in camera sled photographs when their proboscis is extended and they are feeding. Their mean abundances could therefore be much higher even than what is estimated from camera sled photographs.

It is clear that trawls and camera sled photographs yield very different results in terms of mean abundances of many taxa. If it is likely that trawls are overestimating the area sampled, is it also possible that the camera sled

is underestimating the area sampled? For the following reasons, the answer is no: Based on calculations using a Canadian perspective grid, on a level surface the camera sled images approximately 7 m² of the sea floor with 3m² to 4m² clear enough to quantify most of the megafaunal taxa (Wakefield & Genin 1987; Hecker 1992). Also, in the past the camera sled has been tested on land on a laid-out grid, in which the total area in each photograph could be directly measured. Adjustments were then made based on the refractive index of seawater (Dr. Barbara Hecker, personal communication). It is therefore highly probable that the estimated areas in camera sled photographs are indeed fairly accurate.

The camera sled has a number of other strengths. Faunal associations, such as the ophiuroid Asteronyx loveni seen wrapped around a sea whip or other ophiuroids situated at the base of pennatulaceans, are often seen in camera sled photographs.

Patchiness in distribution of invertebrate megafauna is very apparent in camera sled photographs. Certain areas are virtually devoid of epibenthic megafauna while in other areas a multitude of invertebrates can be seen in a single photograph. Large scale patchiness cannot be detected from a single trawl, although it can be estimated by statistical procedures (standard deviation) based on several trawls.

However, smaller scale patchiness cannot be determined by trawls.

Another strength of the camera sled is the ability to record the substrate and other environmental parameters. Mounds, flat areas, rocky outcrops, and fecal casts are all very apparent in camera sled photographs. Hard substrate is seen, often with specific invertebrates associated with it. For example, in this study, a dark green, extremely bifid echiuran was only seen in areas of hard substrate, often in great numbers. This echiuran was not collected in trawls. Conversely a blue-gray echiuran (probably Alomasoma nordpacificum) was only seen in areas of soft substrate.

While the camera sled has some very important strengths, it also has some significant weaknesses. Very small invertebrates are difficult to identify, much less quantify. An entire phylum, Annelida, is not seen in the camera sled photographs as they are primarily small infaunal animals or tube dwellers. Tubes are occasionally seen but it cannot be determined from photographs if the tubes are occupied. Also, infaunal invertebrates are not seen at all, some of which have extremely high densities (e.g., the holothurians of the family Ypsilothuridae and Molpadia spp., as well as the burrowing asteroid Eremicaster pacificus). Also, many invertebrate taxa are not identifiable to species in camera sled photographs. Clearly, trawls are necessary

to sample infaunal invertebrates to allow for invertebrate identification and to provide voucher specimens.

It is interesting to note that of the ranked identifiable species common to camera sled segments and equivalent trawls, the first four rankings were exactly the same for both methods, although in each case the mean abundance was considerably greater in camera sled photographs (Table 10). All four of these species: Paelopadites confundens, Corallimorphus spp., Ophiomusium glabrum, and Pannychia moseleyi are relatively large animals and the first three are quite sturdy. In terms of ranking, at least, it seems that the camera sled and trawls give similar results for the top four epifaunal species.

It is evident that any one method will not adequately sample the deep-sea benthic megafauna. For optimum results a combination of methods, as was used in this study, is necessary.

Summary

The invertebrate megafauna population on the continental slope off of central California is diverse and varied within close geographical distances. The physical factors affecting and regulating the distribution of these invertebrates are poorly understood, as are the life histories of most of these species. Physical factors including upwelling, near-bottom currents, and deposition of detritus probably contribute greatly to variation in species composition among areas. While some seasonal variation was apparent at one site, most of the differences in species composition were related to depth. More rigorous sampling by various methods simultaneously is necessary to adequately describe the invertebrate fauna of this deep-sea area. More research into the biology, particularly the reproductive patterns, of these species would also greatly enhance our understanding of their patterns of abundance and distribution.

LITERATURE CITED

- Aldredge, A.L. & Silver, M.W. 1988. Characteristics, dynamics, and significance of marine snow. Progress in Oceanography. 20: 41-82.
- Aller, J.Y. 1997. Benthic community response to temporal and spatial gradients in physical disturbance within a deep-sea western boundary region. Deep-Sea Research Part I. Oceanographic Research Papers. 44(1): 39-69.
- Alton, M.S. 1966. Bathymetric distribution of sea stars (Asteroidea) off the northern Oregon coast. Journal of the Fisheries Research Board of Canada. 23: 1673-714.
- Alton, M.S. 1972. Bathymetric distribution of echinoderms off the Northern Oregon Coast. In The Columbia River Estuary and Adjacent Ocean Waters, eds. A.T. Pruter & D.L. Alverson, pp. 475-536, Seattle: University of Washington Press.
- Billett, D.S.M. 1991. Deep-sea holothurians. Oceanography and Marine Biology: an Annual Review. 29: 259-317.
- Billett, D.S.M., Lampitt, R.S., Rice, A.L., & Mantoura, R.F.C. 1983. Seasonal sedimentation of phytoplankton to the deep-sea benthos. Nature, London. 302: 520-522.
- Billett, D.S.M., Hansen, B., & Huggett, Q.J. 1984. Pelagic holothuroidea (Echinodermata) of the northeast Atlantic. In Proceedings of the Fifth International Echinoderm Conference, Galway. pp. 399-411.
- Blake, J.A., Muramoto, J., Hilbig, B., & Williams, I.P. 1992. Biological and sedimentological investigations of the sea floor at the proposed U.S. Navy Ocean Disposal Site. July 1991 survey (R/V Wecoma). Benthic biology and sediment characterization. Report prepared for PRC Environmental Management, Inc., under Navy CLEAN Contract No. N62474-88-D-5086.

- Breaker, L.C. & Broenkow, W.W. 1989. The circulation of Monterey Bay and related processes. Moss Landing Marine Laboratories Technical Publication 89-1. 91 pp.
- Carey, A.G., Taghon, L., Stein, D.L., & Rona, P.A. 1990. Distributional ecology of benthic mega-epifauna and fishes in Gorda Ridge Axial Valley. In Gorda Ridge, A Seafloor Spreading Center in the United States Exclusive Economic Zone, ed. G.R. McMurray, pp. 225-240, New York: Springer-Verlag.
- Carney, R.S. and Carey, A.G. 1976. Distribution pattern of holothurians on the northeastern Pacific (Oregon, USA) continental shelf slope and abyssal plain. Thalassia Jugoslavica. 12(1): 67-74.
- Carney, R.S. and Carey, A.G. 1982. Distribution and diversity of holothuroids (Echinodermata) on Cascadia Basin and Tufts Abyssal Plain. Deep-Sea Research. 29(5A): 597-607.
- Child, C. A. 1994. Deep-sea pycnogonida from the temperate west coast of the United States. In Smithsonian Contributions to Zoology. No. 556. Washington, D.C.: Smithsonian Institution Press.
- Eleftheriou, A. and Holme, N.A. 1984. Macrofauna techniques. In Methods for the Study of Marine Benthos. N.A. Holme and A.D McIntyre, eds. Oxford: Blackwell Scientific Publications, pp. 140-216.
- Gage, J.D. and Tyler, P.A. 1991. Deep-Sea Biology: A Natural History of Organisms at the Deep-Sea Floor. New York: Cambridge University Press. 504 pp.
- Haedrich, R.L., Rowe, G.T., & Pollini, P.T. 1975. Zonation and faunal composition of epibenthic populations on the continental slope south of New England. Journal of Marine Research. 33:165-79.

- Haedrich, R.L., Rowe, G.T., & Pollini, P.T. 1980. The megabenthic fauna in the deep sea south of New England, USA. Marine Biology. 57:165-179.
- Hartman, O. and Barnard, J.L. 1958. The benthic fauna of the deep basins off Southern California. Allan Hancock Pacific Expeditions. 22:1-67.
- Hecker, B. 1990a. Variation in megafaunal assemblages on the continental margin south of New England. Deep-Sea Research. 37(1):37-57.
- Hecker, B. 1990b. Photograph evidence for the rapid flux of particles to the sea floor and their transport down the continental slope. Deep-Sea Research. 37(2):1773-1782.
- Hecker Environmental Consulting. 1992. Biological and sedimentological investigations of the sea floor at the proposed U.S. Navy Ocean Disposal Site. July 1991 survey (R/V Wecoma). Megafaunal assemblages. Report prepared for PRC Environmental Management, Inc., under Navy CLEAN Contract No. N62474-88-D-5086.
- Krebs, Charles J. 1989. Ecological Methodology. New York: Harper & Row. 654 pp.
- Lampitt, R.S. 1985. Evidence for the seasonal deposition of detritus to the deep-sea floor and its subsequent resuspension. Deep-Sea Research. 32A: 885-97.
- Lauerman, L.M.L., Kaufmann, R.S., Smith, K.L. Jr. 1996. Distribution and abundance of epibenthic megafauna at a long time series station in the abyssal northeast Pacific. Deep-Sea Research Part I. Oceanographic Papers. 43(7): 1075-1103.
- Maluf, L.Y. 1988. Composition and distribution of the central eastern Pacific echinoderms. Technical Report No.2, Natural History Museum of Los Angeles County. 242 pp.

- Miller, J.E. and Pawson, D.L. 1990. Swimming sea cucumbers (Echinodermata: Holothuroidea): a survey, with analysis of swimming behavior in four bathyal species. Smithsonian Contributions to the Marine Sciences. No. 35, 18 pp.
- Nybakken, J., Smith-Beasley, L., Summers, A., Craig, S., & Weetman, L. 1992a. Invertebrate megafauna collected from the proposed U.S. Navy Ocean Disposal Site as determined from beam and otter trawls and camera sled samples. Report prepared for PRC Environmental Management, Inc., under Navy CLEAN Contract No. N62474-88-D-1991.
- Nybakken, J., Smith-Beasley, L., Summers, A., Craig, S., & Weetman, L. 1992b. Invertebrate megafauna collected from the proposed U.S. Navy Ocean Disposal Site as determined from beam trawls taken in February-March 1992. Supplementary report prepared for PRC Environmental Management, Inc., under Navy CLEAN Contract No. N62474-88-D-1991.
- Ohta, S. 1983. Photographic census of large-sized benthic organisms in the bathyal zone of Suruga Bay, central Japan. Bulletin of the Ocean Research Institute. University of Tokyo, No. 15, 244 pp.
- Pawson, D.L. and Foell, J. 1986. Peniagone leander new species, an abyssal benthopelagic sea cucumber (Echinodermata: Holothuroidea) from the Eastern Central Pacific Ocean. Bulletin of Marine Science. 38(2): 293-299.
- Pearson, M. & Gage, J.D. 1984. Diets of some brittle stars in the Rockall Trough. Marine Biology. 82: 247-58.
- Pielou, E.C. 1966. The measurement of diversity in different types of biological collections. Journal of Theoretical Biology. 13: 131-144.
- Rokop, F.J. 1974. Reproductive patterns in deep-sea benthos. Science, Washington. 186:743-5.

- Shimek, R.L. and Moreno, G. 1996. A new species of eastern Pacific Fissidentalium (Mollusca: Scaphopoda). Veliger. 39 (1): 71-82.
- Smith, C.R. 1985a. Food for the deep-sea: utilization, dispersal and flux of nekton falls at the Santa Catalina Basin floor. Deep-Sea Research. 32A:417-42.
- Smith, C.R. 1994. Tempo and mode in deep-sea benthic ecology: Punctuated equilibrium revisited. Palaios. 9(1): 3-13.
- Smith, C.R. and Hamilton, S.C. 1983. Epibenthic megafauna of a bathyal basin off southern California: patterns of abundance, biomass, and dispersion. Deep-Sea Research. 30:907-928.
- Smith, K.L. Jr., Kaufmann, R.S., & Baldwin, R.J. 1994. Coupling of near-bottom pelagic and benthic processes at abyssal depths in the eastern North Pacific Ocean. Limnology and Oceanography. 39(5): 1101-1118.
- Summers, A.C. 1993. Bathymetric, spatial, and local zoogeographic distribution of ophiuroids on the continental slope off central California. Moss Landing, CA: Moss Landing Marine Laboratories. Thesis.
- Thiel, H., Pfannkuche, O., Schriever, G., Lochte, K. Gooday, A.J., Hemleben, C., Mantoura, R.F.G., Patching, O., Turley, C.M. & Riemann, F. 1988. Phytodetritus on the deep-sea floor in a central oceanic region of the northeast Atlantic. Biological Oceanography. 6: 203-39.
- Thurston, M.H., Bett, B.J., Rice, A.L., Jackson, P.A.B. 1994. Variations in the invertebrate abyssal megafauna in the North Atlantic Ocean. Deep-Sea Research Part I. Oceanographic Research Papers. 41(9): 1321-1348.
- Tyler, P.A. 1980. Deep-sea ophiuroids. Oceanography and Marine Biology: an Annual Review. 18: 125-53.

- Tyler, P.A. 1986. Studies of benthic time-series: reproductive biology of benthic invertebrates in the Rockall Trough. Proceedings of the Royal Society of Edinburgh. 88B: 175-90.
- Tyler, P.A. 1988. Seasonality in the deep-sea. Oceanography and Marine Biology: an Annual Review. 26: 227-258.
- Uzmann, J.R., Cooper, R.A., Theroux, R.B., & Wigley, R.L. 1977. Synoptic comparison of three sampling techniques for estimating abundance and distribution of selected megafauna: submersible VS camera sled VS otter trawl. Marine Fisheries Review. 39:11-19.
- Wakefield, W.W. and Genin, A. 1987. The use of a Canadian (perspective) grid in deep-sea photography. Deep-Sea Research. 34A: 469-78.
- Wolda, H. 1981. Similarity indices, sample size and diversity. Oecologia. 50:296-302.

Table 1. Beam and otter trawl data from the Farallon site in 1991.

TRAWL #	TRAWL TYPE	DATE (1991)	DEPTH (m)	POSITION (on bottom) (N)	POSITION (off bottom) (W)	BOTTOM TIME (on-off)	DURATION (minutes)	DIST-ANCE (nm)	AREA TOWED (m ²)
11-1	Beam	27 July	2,975-3,010	37°38.45'/123°29.83'	37°38.53'/123°29.23'	01:41-02:04	23	0.48	1,867
11-2	Beam	27 July	2,795-2,865	37°38.90'/123°27.96'	37°39.56'/123°27.00'	06:32-07:18	46	1.01	3,928
11-3	Beam	27 July	2,850-2,910	37°38.42'/123°28.60'	37°39.14'/123°27.52'	11:28-12:23	55	1.12	4,356
11-4	Beam	27 July	2,945-3,075	37°37.35'/123°30.61'	37°37.55'/123°29.63'	16:03-16:43	40	0.80	3,111
11-5	Beam	27 July	2,840-3,075	37°38.62'/123°28.03'	37°39.05'/123°27.18'	20:35-21:40	45	0.80	3,111
11-6	Otter	28 July	2,760-2,865	37°38.97'/123°27.70'	37°39.61'/123°26.59'	03:16-04:09	53	1.09	11,789
11-7	Otter	28 July	---	NO FISHING	----	----	--	--	---
11-8	Otter	28 July	2,760-2,875	37°37.58'/123°29.27'	37°38.07'/123°27.04'	15:45-16:50	65	1.83	19,793
11-9	Beam	28 July	2,775-2,840	37°39.05'/123°27.36'	37°39.20'/123°25.60'	21:20-22:41	81	1.40	5,445
11-10	Beam	29 July	2,605-2,760	37°39.20'/123°25.38'	37°38.85'/123°23.94'	03:00-03:53	53	1.19	4,628
11-11	Beam	29 July	2,470-2,570	37°38.86'/123°23.67'	37°38.83'/123°22.00'	07:44-08:40	56	1.32	5,134
11-12	Beam	29 July	2,300-2,375	37°38.40'/123°21.53'	37°38.36'/123°19.90'	12:20-13:10	83	1.29	5,017
11-13	Beam	29 July	---	RADIOACTIVE	----	----	--	--	---
11-14	Beam	30 July	2,690-3,015	37°34.99'/123°30.07'	37°35.03'/123°28.75'	01:13-02:05	52	1.05	4,084
11-15	Otter	30 July	---	NO FISHING	----	----	--	--	---
11-16	Beam	30 July	2,900-3,000	37°37.50'/123°29.98'	37°37.79'/123°29.03'	13:50-14:35	45	0.81	3,150

Table 2. Beam trawl data from the Farallon, Pioneer Canyon, and Monterey Canyon sites, 1992.

TRAWL#	SITE	DATE (1992)	DEPTH (m)	POSITION (N bottom) (N) (W)	POSITION (off bottom) (N) (W)	BOTTOM TIME (on-off)	DURATION (min)	DIST- ANCE (nm)	AREA TOWED (m ²)
F-1	Farallones	27 Feb	2,850-2,990	37°39.47'/123°30.19'	37°39.51'/123°28.34'	20:40-21:33	53	1.47	5,717
F-2	Farallones	27 Feb	----	NET RIPPED	----	---	--	--	--
F-3	Farallones	28 Feb	2,890-2,970	37°38.05'/123°29.62'	37°38.34'/123°28.62'	07:03-07:40	37	0.84	3,267
F-4	Farallones	28 Feb	2,900-3,000	37°39.24'/123°30.79'	37°39.35'/123°29.34'	10:53-11:43	50	1.15	4,473
F-5	Farallones	28 Feb	2,850-2,950	37°39.07'/123°29.79'	37°39.53'/123°28.96'	15:57-16:32	35	0.80	3,111
P-1	Pioneer	28 Feb	3,150-3,280	37°04.35'/123°26.42'	37°04.75'/123°25.89'	23:38-00:02	24	0.58	2,256
P-2	Pioneer	29 Feb	3,190-3,200	37°05.36'/123°24.91'	37°05.61'/123°23.97'	03:54-04:33	39	0.79	3,072
P-3	Pioneer	29 Feb	3,090-3,300	37°03.27'/123°26.30'	37°03.97'/123°25.26'	08:17-09:07	50	1.09	4,239
P-4	Pioneer	29 Feb	3,175-3,180	37°04.44'/123°24.40'	37°04.72'/123°23.77'	11:57-12:35	38	0.58	2,256
M-1	Monterey	1 Mar	2,820-2,960	36°15.94'/122°36.66'	36°16.71'/122°36.41'	10:14-10:47	33	0.80	3,111
M-2	Monterey	1 Mar	2,650-2,680	36°16.57'/122°35.61'	36°17.67'/122°35.53'	13:39-14:25	46	1.10	4,278
M-3	Monterey	1 Mar	2,620-2,800	36°20.30'/122°36.17'	36°19.19'/122°35.85'	17:03-17:59	56	1.14	4,434
M-4	Monterey	1 Mar	2,630-2,790	36°18.39'/122°36.44'	36°19.77'/122°35.71'	20:25-21:29	64	1.50	5,834
M-5	Monterey	1 Mar	3,250-3,270	36°23.88'/122°39.27'	36°24.98'/122°38.60'	00:22-01:17	55	1.23	4,784
M-6	Monterey	2 Mar	3,150-3,200	36°25.71'/122°37.69'	36°27.05'/122°37.51'	04:05-05:11	66	1.35	5,250
M-7	Monterey	2 Mar	2,810-2,900	36°26.53'/122°30.71'	36°27.72'/122°30.81'	08:15-09:12	57	1.19	4,628
M-8	Monterey	2 Mar	2,800-2,900	36°26.61'/122°30.73'	36°27.67'/122°30.71'	11:49-12:48	59	1.06	4,123

Table 3. Presence of species/taxa at the Farallon 1991/1992, Pioneer Canyon, and Monterey Canyon sites.

SPECIES/TAXA	F 1991	F 1992	PC 1992	MC 1992
PORIFERA				
Hexactinellidae unidentified		X	X	
Porifera unidentified	X	X		
CNIDARIA				
Order Gorgonacea				
Unidentified gorgonians	X	X	X	X
Order Pennatulacea				
Kophobelemnion cf. stelliferum	X	X	X	X
Kophobelemnion cf. affine	X	X	X	X
Pennatula phosphorea	X	X		
Distichoptilum gracile	X			
Stachyptilum sp. indet.	X			
Order Alcyonacea				
Anthomastus ritteri		X		
Order Actiniaria				
Actinauge verrilli	X	X		
Actinernus sp.	X	X		
Actinoscyphia sp.	X	X		
Actinostola sp.				X

Table 3 continued.

Order Actiniaria cont.	F 1991	F 1992	PC 1992	MC 1992
Bolocera sp.	X			
Paractinostola faeculenta	X			
Sicyonis sp.	X	X		
Actinostolidae	X	X		
Edwardsiidae	X			X
Hormathia sp.	X			
Hormathiidae		X		X
Hormathia digitata		X		
Paraphelliactis pabista			X	
Liponema brevicornis	X			X
Anemones unidentified	X	X	X	X
Order Corallimorpharia				
Corallimorphus spp.	X	X	X	X
Order Scleractinia				
Fungiacyathus marenzelleri	X	X		
Order Antipatharia				
Antipatharia unidentified		X		X
MOLLUSCA				
Class Polyplacophora				
Leptochiton alveolus	X	X		X

Table 3 continued.

Class Gastropoda	F1991	F1992	PC1992	MC1992
Lepeta caecoides	X			
Lunatia pallida	X	X	X	X
Buccinum diplodetum	X			
Colus jordani	X	X	X	X
Colus cf. trophius	X			
Colus sp. A		X		X
Aforia cf. goodei	X			
Steiraxis aulaca	X	X	X	X
Opisthobranch sp. 1	X	X		X
Class Bivalvia				
Eunucula cardara				X
Malletia cf. talama	X	X	X	X
Nuculana pontonia				X
Acharax johnsoni	X	X		X
Vesicomya (Calyptogena) pacifica				X
Cardiomya pectinata	X			
Cardiomya planetica				
Cuspidaria glacialis	X	X	X	X
Dalliocordia alaskana				X
Policordia alaskana	X			X

Table 3 continued.

Class Scaphopoda	F1991	F1992	PC1992	NC1992
Fissidentalium megathyris	X	X	X	X
Fissidentalium erosum (new species)			X	
Class Cephalopoda				
Benthoctopus sp.	X			
Graneledone pacifica	X			X
Vampyroteuthis infernalis	X			
ANNELIDA				
Class Polychaeta				
Aphrodita cf. japonica	X	X	X	X
Laetmonice ?pellucida	X	X		
Glycera cf. robusta	X		X	X
Goniada cf. maculata			X	
Austrophyllium exsilium			X	
Eulalia lapsus			X	
Sige brunnea			X	
Chaetoparia sp. A	X			
Phyllodocidae unid.	X			
Polaruschakov sp. A			X	
Polynoidae unid.	X			
Anchinotria sp. A	X	X	X	X

Table 3 continued.

Class Polychaeta cont.	F 1991	F 1992	PC 1992	MC 1992
Onuphis vibex				X
Paradiopatra sp. A	X	X	X	X
Lumbrineris sp. F		X	X	X
Lumbrineris sp.	X		X	X
?Orbinidae unid.				X
Aricidea (Acmira) simplex		X		X
Levinisenia gracilis			X	
Spiophanes fimbriata	X		X	X
Spiophanes sp. unid.		X		
Amage arieticornuta	X		X	
Ampharete arctica			X	
Anobothrus mancus	X		X	
Ecamphicteis elongata			X	
Melinna sp. A	X	X	X	X
Melinna sp. B			X	
Melinnampharete gracilis	X		X	
Paralysippe annectans			X	
Amphitrite cirrata				X
Amphitritinae unid.				
Terebellides kobei	X		X	
?Thelepus	X			

Table 3 continued.

Class Polychaeta cont.	F 1991	F 1992	PC 1992	MC 1992
Phyllochaetopterus limicolus	X	X	X	X
Ilyphagus ilyvestis				X
Fauvelopsis cf. glabra			X	
Clymaldane laevis		X		X
Euclymeninae sp.			X	
?Lumbriclymene sp.			X	
Maldane monilata	X	X	X	X
Clymenura sp.	X			
Maldanidae unid.			X	
Sonatsa meridionalis			X	
Capitellidae Genus A			X	X
Travisia pupa			X	
Travisia sp. A			X	X
Myriochele sp. unid.			X	X
Euchone sp. D			X	
Sabellidae unid.	X			
?Pseudoscalibregma sp. A		X		

Table 3 continued.

ARTHROPODA	F 1991	F 1992	PC 1992	MC 1992
Class Pycnogonida				
<i>Ascorhynchus japonica</i>				X
<i>Colossendeis colossea</i>	X			X
<i>Colossendeis macerrima</i>	X	X	X	X
<i>Colossendeis tenera</i>	X	X	X	X
<i>Colossendeis peloria</i> (new species)				X
<i>Nymphon aculeatum</i>	X	X		X
<i>Pallenopsis comosa</i>	X		X	
<i>Pallenopsis longiseta</i>		X		X
Class Malacostraca				
<i>Storothyngura bicornis</i>			X	
<i>Amphipoda</i> unid.				X
<i>Benthesicymus tanneri</i>	X			
<i>Crangon abyssorum</i>	X	X	X	X
<i>Munidopsis latirostris</i>			X	X
<i>Munidopsis verrilli</i>	X	X	X	X
<i>Paralomis verrilli</i>	X			
<i>Anomuran</i> sp. 1	X			
<i>Gymnoscalpellum</i> sp.				X

Table 3 continued.

ECHIURA	F 1991	F 1992	PC 1992	MC 1992
Alomasoma nordpacificum	X	X	X	X
Choanostomellia bruuni	X	X	X	X
Unidentified echiurian			X	X
ECHINODERMATA				
Class Crinoidea				
Unidentified crinoids		X		X
Class Asteroidea				
Psilaster pectinatus	X			X
Psilaster cf. pectinatus				X
Benthopecten acanthonotus	X	X		X
Eremicaster gracilis			X	X
Eremicaster pacificus	X	X	X	X
Pseudarchaster dissonus	X			X
Pseudarchaster parelli	X			
Pseudarchaster pusillus				X
Henricia asthenactis		X		
Hymenaster koehleri	X	X	X	X
Hymenaster perissonotus	X			
Hymenaster quadrispinosus	X	X	X	X
Lophaster furcilliger		X		

Table 3 continued.

Class Asteroidea cont.	F 1991	F 1992	PC 1992	MC 1992
Solaster sp. indet.	X			
Brisingidae - unidentified spp.	X	X		X
Cnemidaster nudus	X			X
Cnemidaster wyvillii	X			
Zoroaster evermanni	X			
Zoroaster evermanni mordax	X			
Zoroaster sp. (juvenile)	X			
Class Ophiuroidea				
Asteronyx loveni	X	X		X
Amphilepis platytata	X	X	X	X
Amphiura carchara	X	X	X	X
Amphiura diomedea	X	X	X	X
Amphiura otteri	X	X	X	X
Ophiacantha eurypona		X		
Ophiacantha cf. pacifica			X	X
Ophiolimna bairdi	X	X		X
Ophiocten hastatum	X	X	X	X
Ophiomusium glabrum	X			X
Ophiura bathybia	X	X	X	
Ophiura leptoctenia	X	X		
Class Echinoidea				
Tromikosoma panamense	X	X	X	X
Urechinus sp.	X			
Aeropsis fulva	X	X	X	X
Class Holothuroidea				
Echinocucumis hispida	X	X	X	X
Ypsilothuria bitentaculata	X	X	X	X
Abyssocucumis albatrossi	X			X

Table 3 continued.

Class Holothuroidea cont.	F 1991	F 1992	PC 1992	MC 1992
<i>Psolidium gracile</i>		X		X
<i>Paelopadites confundens</i>	X	X		X
<i>Synallectes aenigma</i>	X			
<i>Elpidia</i> sp. cf. <i>theeli</i>				X
<i>Peniagone</i> cf. <i>incerta</i>				X
<i>Scotoplanes globosa</i>	X	X	X	X
<i>Pannychia moseleyi</i>	X			
<i>Benthodytes sanguinolenta</i>	X			X
<i>Molpadia bathybia</i>		X		
<i>Molpadia intermedia</i>	X	X	X	X
<i>Molpadia musculus</i>	X	X	X	X
<i>Protankyra abyssicola</i>	X	X	X	X
<i>Anapta</i> sp. indet. (new species)		X		X
Unidentified sp.	X			

Table 4. Percent similarity among trawl sites and between equivalent camera sled segments and F1991 trawls. Calculated as sum of minimums (Krebs 1989).

(*Percent similarity between the 25 most common species from F 1991 compared to F 1992.)

	Farallon 1991 (camera sled)	Farallon 1992	Pioneer Canyon 1992	Monterey Canyon 1992 2620-3270 m
Farallon 1991 2300-3075 m	40	69 *(66)	44	39
Farallon 1992 2850-3000 m			46	42
Pioneer Canyon 1992 3090-3300 m				33

Table 5. Comparison (by percentage) of the 25 most abundant species from the Farallon 1991 trawls with Farallon 1992 trawls. Percent similarity = 66% (Krebs 1989).

SPECIES	F 1991	F 1992
Ypsilothuridae	29.6	37.7
Paelopadites confundens	11.9	2.7
Amphiura carchara	8.73	11.9
Molpadia intermedia	6.61	5.15
Corallimorphus spp.	5.75	1.43
Eremicaster pacificus	5.51	5.22
Amphilepis platytata	4.86	4.54
Kophobelemnon cf. stelliferum	2.42	3.93
Ophiomusium glabrum	1.83	0
Paradiopatra sp. A	1.46	1.61
Pannychia moseleyi	1.41	0
Aphrodita cf. japonica	1.26	4.77
Maldane monilata	1.13	1.51
Alomasoma nordpacificum	1.06	1.88
Tromikosoma panamense	0.95	0.16
Ophiocten hastatum	0.85	2.23
Psilaster pectinatus	0.81	0
Amphiura diomedae	0.74	1.34
Pennatula phosphorea	0.73	0
Benthopecten acanthonotus	0.71	0.07
Kophobelemnon cf. affine	0.67	0.25
Protankyra abyssicola	0.67	0.52
Fissidentulum megathyris	0.61	0.86
Ophiolimna bairdi	0.51	1.52
Colossendeis tenera	0.46	0.16
PERCENT OF ALL SPECIMENS	0.91	0.89

Table 6. Species found at all study sites.

CNIDARIA:		ECHIUURA:	
Order Pennatulacea		Family Bonelliidae	
	<i>Kophobelemnion</i> cf. <i>stelliferum</i>		<i>Alomasoma nordpacificum</i>
	<i>Kophobelemnion</i> cf. <i>affine</i>		<i>Choanostomellia bruuni</i>
Order Corallimorpharia			
	<i>Corallimorphus</i> spp.		
MOLLUSCA:		ECHINODERMATA:	
Class Gastropoda		Class Asteroidea	
	<i>Lunatia pallida</i>		<i>Eremicaster pacificus</i>
	<i>Colus jordani</i>		<i>Hymenaster koehleri</i>
	<i>Steiraxis aulaca</i>		<i>Hymenaster quadrispinosus</i>
Class Bivalvia		Class Ophiuroidea	
	<i>Malletia</i> cf. <i>talama</i>		<i>Amphilepis platytata</i>
	<i>Cuspidaria glacialis</i>		<i>Amphiura carchara</i>
Class Scaphopoda			<i>Amphiura diomedea</i>
	<i>Fissidentalium megathyris</i>		<i>Amphiura otteri</i>
			<i>Ophiocten hastatum</i>
ANNELIDA:		Class Echinoidea	
Class Polychaeta			<i>Tromikosoma panamense</i>
	<i>Aphrodita</i> cf. <i>japonica</i>		<i>Aeropsis fulva</i>
	<i>Anchinothria</i> sp. A	Class Holothuroidea	
	<i>Paradiopatra</i> sp. A		<i>Echinocucumis hispida</i>
	<i>Melinna</i> sp. A		<i>Ypsilothuria bitentaculata</i>
	<i>Phyllochaetopterus limicolus</i>		<i>Scotoplanes globosa</i>
	<i>Maldane monilata</i>		<i>Molpadia intermedia</i>
			<i>Molpadia musculus</i>
			<i>Protankyra abyssicola</i>
ARTHROPODA:			
Class Pycnogonida			
	<i>Colossendeis macerrima</i>		
	<i>Colossendeis tenera</i>		
Class Malacostraca			

Table 7. Species found at only one study site.

CNIDARIA:

Order Pennatulacea

Distichoptilum gracile - F 1991

Stachyptilum sp. indet. - F 1991

Order Alcyonacea

Anthomastus ritteri - F 1992

Order Actiniaria

Actinstola sp. - MC 1992

Bolocera sp. - F 1991

Paractinostola faeculenta - F 1991

Edwardsiidae unidentified - F 1991

Hormathia digitata - F 1992

Hormathidae unidentified - F 1992

Paraphelliactis pabista - PC 1992

MOLLUSCA:

Class Gastropoda

Lepeta caecoides - F 1991

Buccinum diplodetum - F 1991

Colus cf. *trophius* - F 1991

Aforia cf. *goodei* - F 1991

Class Bivalvia

Cardiomya pectinata - F 1991

Cardiomya planetica - MC 1992

Eunnucula cardara - MC 1992

Nuculana pontonia - MC 1992

Vesicomya pacifica - MC 1992

Dalliocordia alaskana - MC 1992

Class Scaphopoda

Fissidentalium erosum (new species) - PC 1992

Class Cephalopoda

Benthoctopus sp. - F 1991

Vampyroteuthis infernalis - F 1991

ANNELIDA:

Class Polychaeta

Chaetoparia sp. A - F 1991

Phyllodocidae unidentified - F 1991

Polynoidae unidentified - F 1991

Terebellides kobei - F 1991

?*Thelepus* - F 1991

Clymenura sp. - F 1991

Sabellidae unidentified - F 1991

Spiophanes sp. unid. - F 1992

?*Pseudoscalibregma* sp. A - F 1992

Goniada cf. *maculata* - PC 1992

Table 7 continued.

Class Polychaeta (cont.)

Austrophyllum exsilium - PC 1992
Eulalia lapsus - PC 1992
Sige brunnea - PC 1992
Polaruschkov sp. A - PC 1992
Levinsenia gracilis - PC 1992
Ampharete arctica - PC 1992
Ecamphicteis elongata - PC 1992
Melinna sp. B - PC 1992
Paralysippe annectans - PC 1992
Amphitritinae unidentified - PC 1992
Fauveliopsis cf. *glabra* - PC 1992
Euclymeninae unidentified - PC 1992
? *Lumbriclymene* sp. - PC 1992
Maldanidae unidentified - PC 1992
Sonatsa meridionalis - PC 1992
Travisia pupa - PC 1992
Euchone sp. D - PC 1992
Onuphis vibex - MC 1992
?Orbinidae unidentified - MC 1992
Amphitrite cirrata - MC 1992
Ilyphagus ilyvestis - MC 1992

ARTHROPODA:

Class Pycnogonida

Ascorhynchus japonica - MC 1992
Colossendeis peloria (new species) - MC 1992

Class Malacostraca

Benthescicymus tanneri - F 1991
Paralomis verrilli - F 1991
Anomuran sp. 1 - F 1991
Storothyngura bicornis - PC 1992
Amphipoda unidentified - MC 1992
Gymnoscalpellum sp. - MC 1992

ECHINODERMATA:

Class Asteroidea

Pseudarchaster parelli - F 1991
Hymenaster perissonotus - F 1991
Solaster sp. indet. - F 1991
Cnemidaster wyvilli - F 1991
Zoroaster evermanni - F 1991
Zoroaster evermanni mordax - F 1991
Zoroaster sp. - F 1991
Henricia asthenactis - F 1992
Lophaster furcilliger - F 1992

Table 7 continued.

Class Asteroidea (cont.)

Psilaster cf. *pectinatus* - MC 1992

Pseudarchaster pusillus - MC 1992

Class Ophiuroidea

Ophiacantha eurypoma - F 1992

Class Echinoidea

Urechinus sp. - F 1991

Class Holothuroidea

Synallectes aenigma - F 1991

Pannychia moseleyi - F 1991

Molpadia bathybia - F 1992

Elpidia sp. cf. *theeli* - MC 1992

Peniagone cf. *incerta* - MC 1992

Table 8. Number of species/taxa per polychaete family at at the Farallon 1991/1992, Pioneer Canyon, and Monterey Canyon sites.

Family	F 1991	F 1992	PC 1992	MC 1992
Aphroditidae	2	2	1	1
Glyceridae	1	0	1	1
Goniadidae	0	0	1	0
Phyllodocidae	2	0	3	0
Polynoidae	1	0	1	0
Onuphidae	2	2	2	3
Lumbrineridae	1	1	2	2
Orbiniidae	0	0	0	1
Paraonidae	0	1	1	1
Spionidae	1	1	1	1
Ampharetidae	4	1	8	1
Terebellidae	2	0	1	1
Chaetopteridae	1	1	1	1
Flabelligeridae	0	0	0	1
Fauveliopsidae	0	0	1	0
Maldanidae	2	2	5	2
Capitellidae	0	0	1	1
Opheliidae	0	0	2	1
Scalibregmidae	0	1	0	0
Oweniidae	0	0	1	1
Sabellidae	1	0	1	0
	n=367	n=398	n=852	n=567

Table 9. Ranked taxa and Spearman's rank (r_s) of camera sled segments and equivalent trawls (N=11), in mean number of individuals per 100 m² ($r_s=.63$ [0.05 < P < 0.10]).

TAXA	Sled	Rank	Trawl	Rank
Sea Pens	209.34	1	0.5	5
Anemones	17.45	3	0.65	4
Molluscs	0.357	9	0.11	9
Arthropods	5.38	5	0.24	6
Echiurans	5.08	6	0.19	7
Asteroids	1.06	7	0.9	3
Ophiuroids	69.08	2	2.2	2
Echinoids	0.39	8	0.13	8
Holothurians	14.04	4	5.3	1
Total per 100m ²	322.17	—	10.22	—

Table 10. Ranked identifiable species/taxa and Spearman's Rank (r_s) of camera sled segments and equivalent trawls (N=11) in mean number of individuals per 100 m² ($r_s = .45$ [$0.05 < p < 0.10$]).

SPECIES/TAXA	Sled	Rank	Trawl	Rank
<i>Paelepadites confundens</i>	7.74	1	1.31	1
<i>Corallimorphus</i> spp.	7.46	2	0.567	2
<i>Pannychia moseleyi</i>	5.07	3	0.342	3
<i>Ophiomusium glabrum</i> .	1.66	4	0.289	4
<i>Asteronyx loveni</i>	0.956	5	0.036	7
<i>Tromikosoma panamense</i>	0.605	6	0.122	5
<i>Munidopsis verrilli</i>	0.59	7	0.011	13
<i>Liponema brevicornis</i>	0.58	8	0.002	17
Zoroasteridae	0.381	9	0.016	12
<i>Paractinostola faeculenta</i>	0.322	10	0.005	15
<i>Benthodytes sanguinolenta</i>	0.24	11	0.001	18
Pterasteridae	0.211	12	0.024	9
Brsingidae	0.157	13	0.004	16
Actinostolidae	0.136	14	0.019	11
<i>Paralomis verrilli</i>	0.135	15	0.035	8
Solasteridae	0.125	16	0.006	14
Goniasteridae	0.075	17	0.02	10
<i>Benthopecten acanthonotus</i>	0.018	18	0.044	6

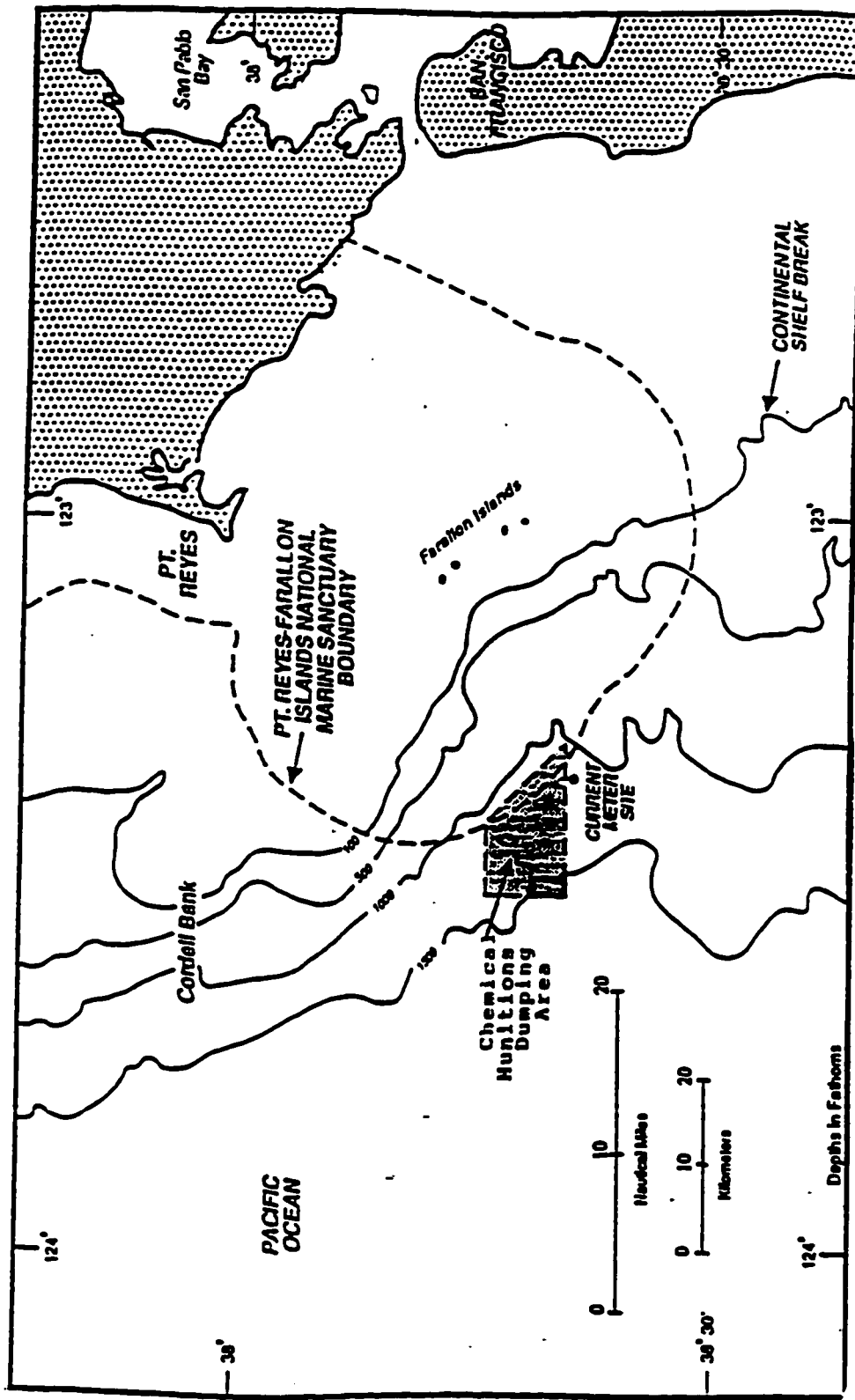


Figure 1. Location of the Chemical Munitions Dumping Area off the Farallon Islands. The small rectangle is the Navy Ocean Disposal Site (NODS). Trawls were taken at this location in July/August 1991 and February 1992 (from Nybakken et al., 1992a).

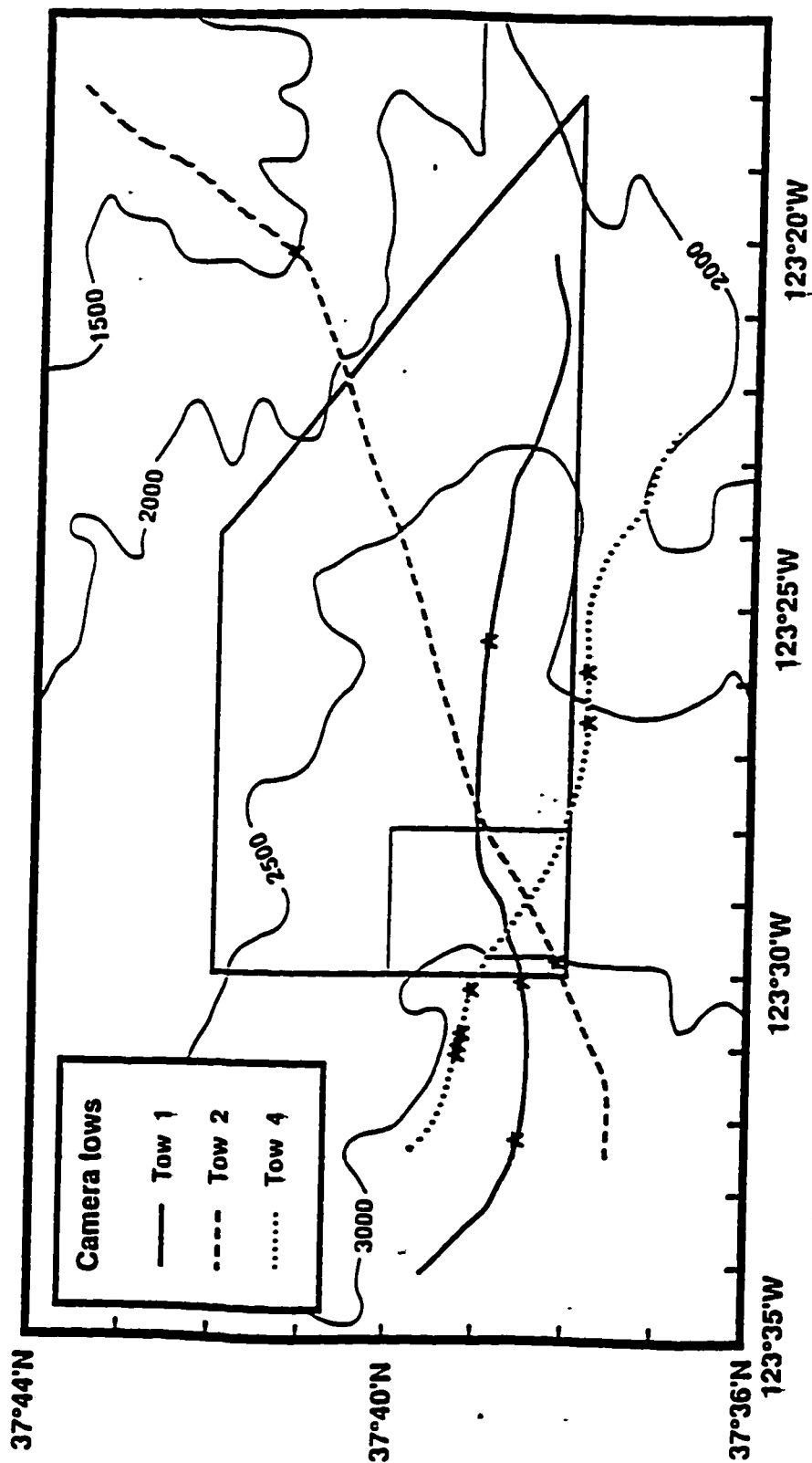


Figure 2. Location of camera sled tows for the study of megafaunal invertebrate populations off the Farallon slope. The trapezoid is the former Chemical Munitions Dumping Area (CMDA). The small rectangle is the Navy Ocean Disposal Site (NODS). Stars represent rock outcrops. Contours are in meters. (From Hecker, 1992; used with permission.)

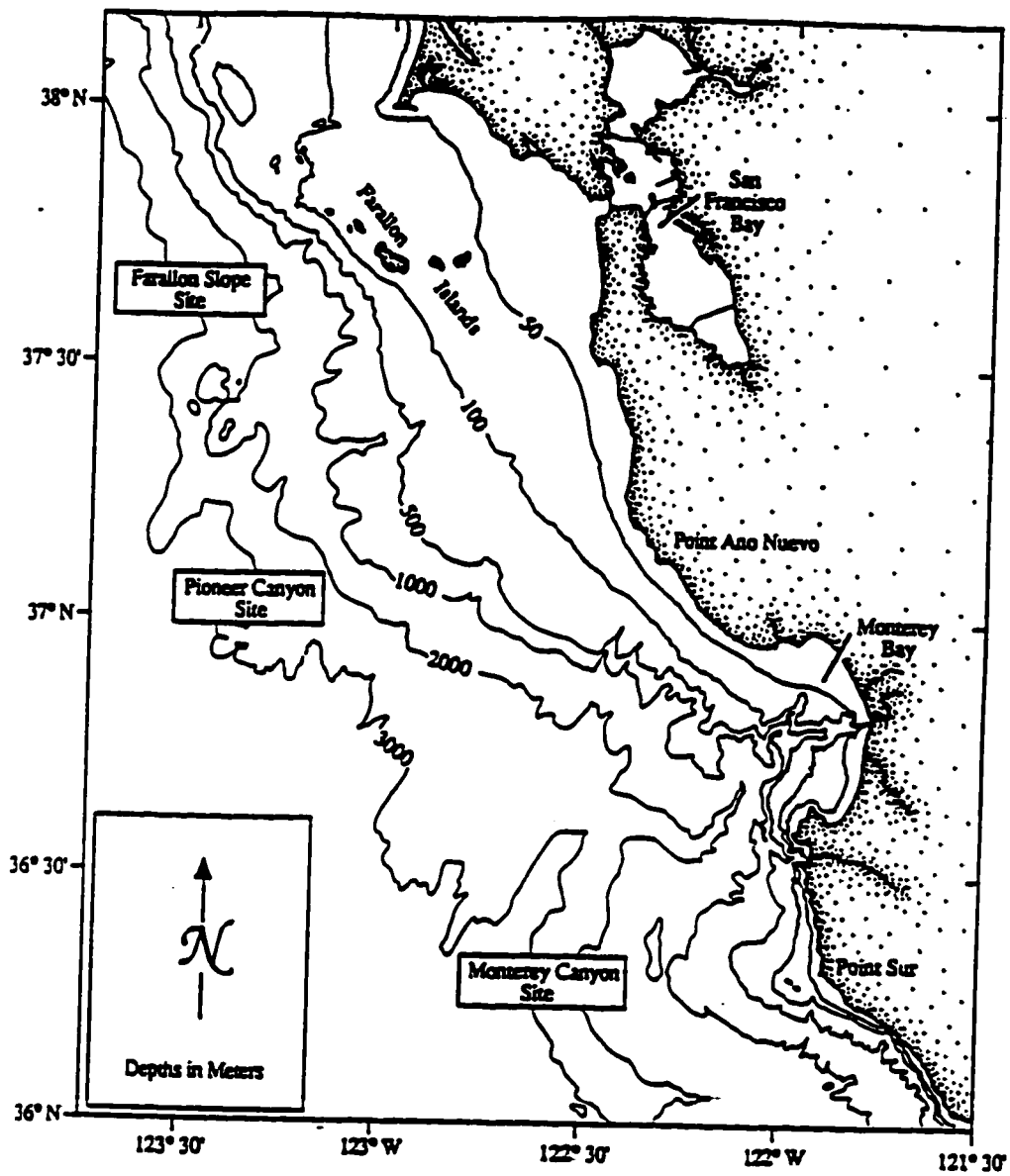


Figure 3. Map of the Farallon Slope, Pioneer Canyon, and Monterey Canyon study sites off the central California coast. (From Summers, 1993; used with permission.)

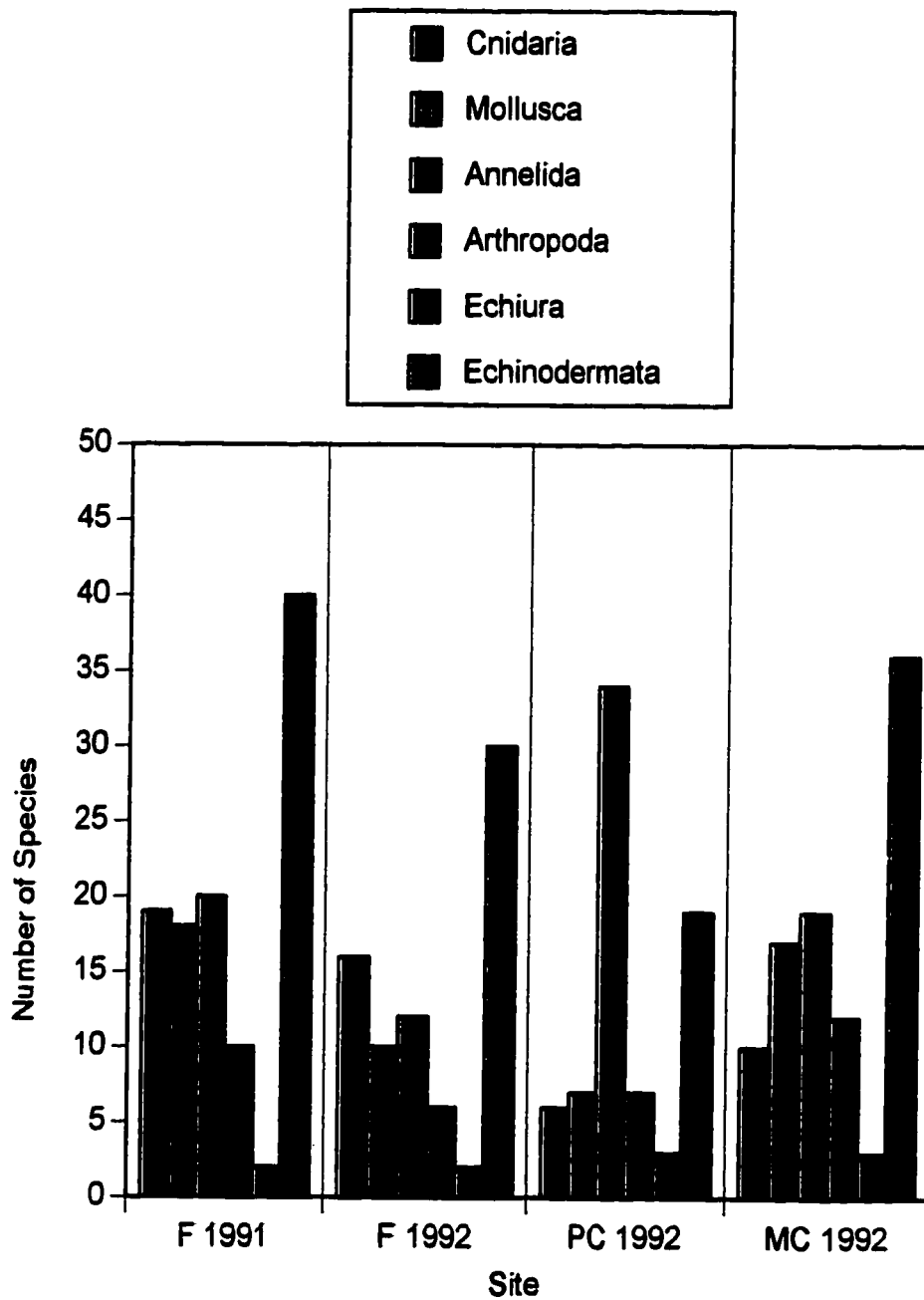


Figure 4. Comparison of the number of species/taxa per phylum collected with trawls at the Farallon 1991/1992, Pioneer Canyon, and Monterey Canyon sites.

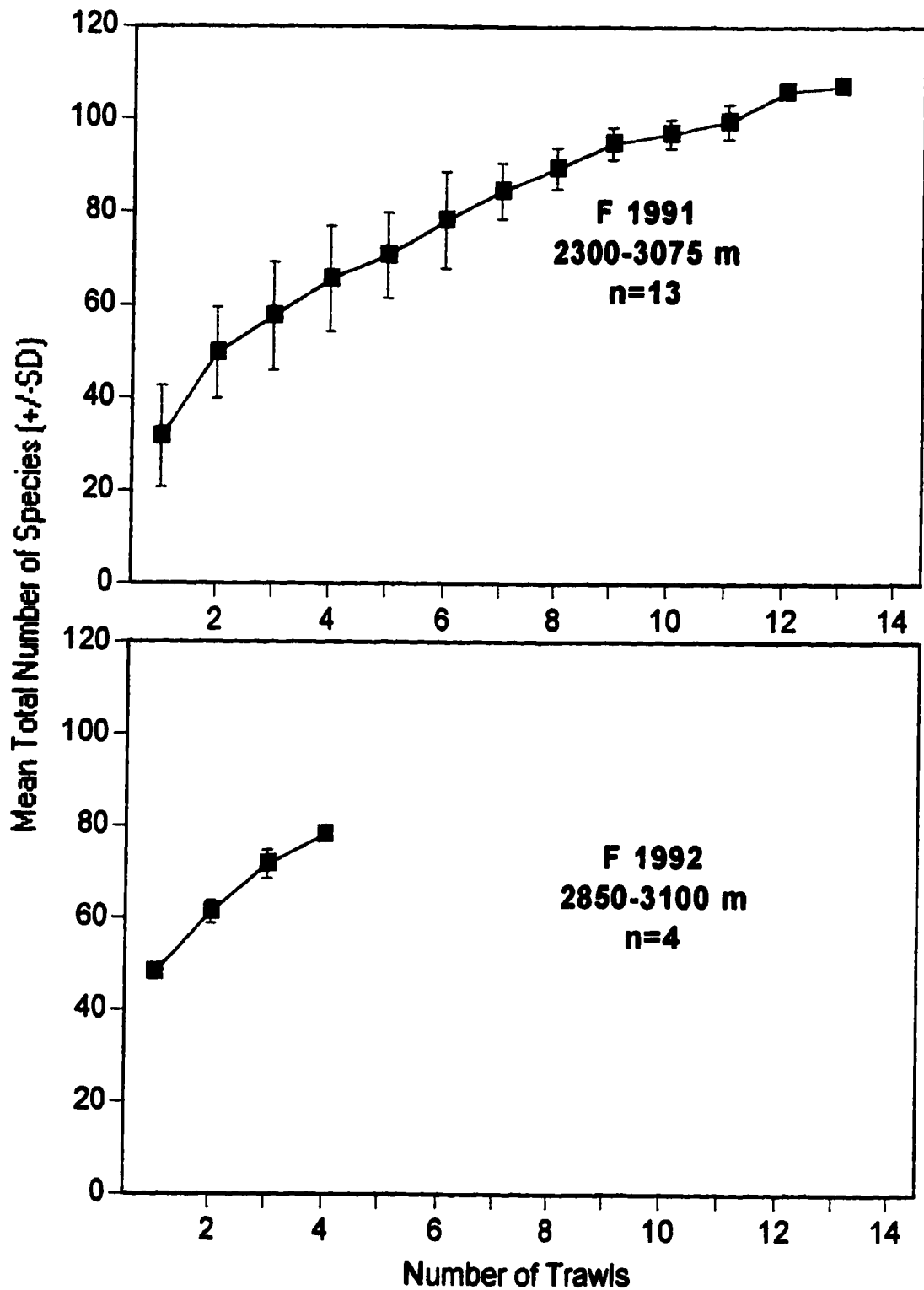


Figure 5. Cumulative species curves for invertebrate megafauna collected with trawls at the Farallon site in 1991 and 1992. There were 13 trawls at the Farallon site in 1991 and 4 trawls at the Farallon site in 1992. Each value is the mean cumulative number of species +/-the standard deviation for 10 random combination of samples.

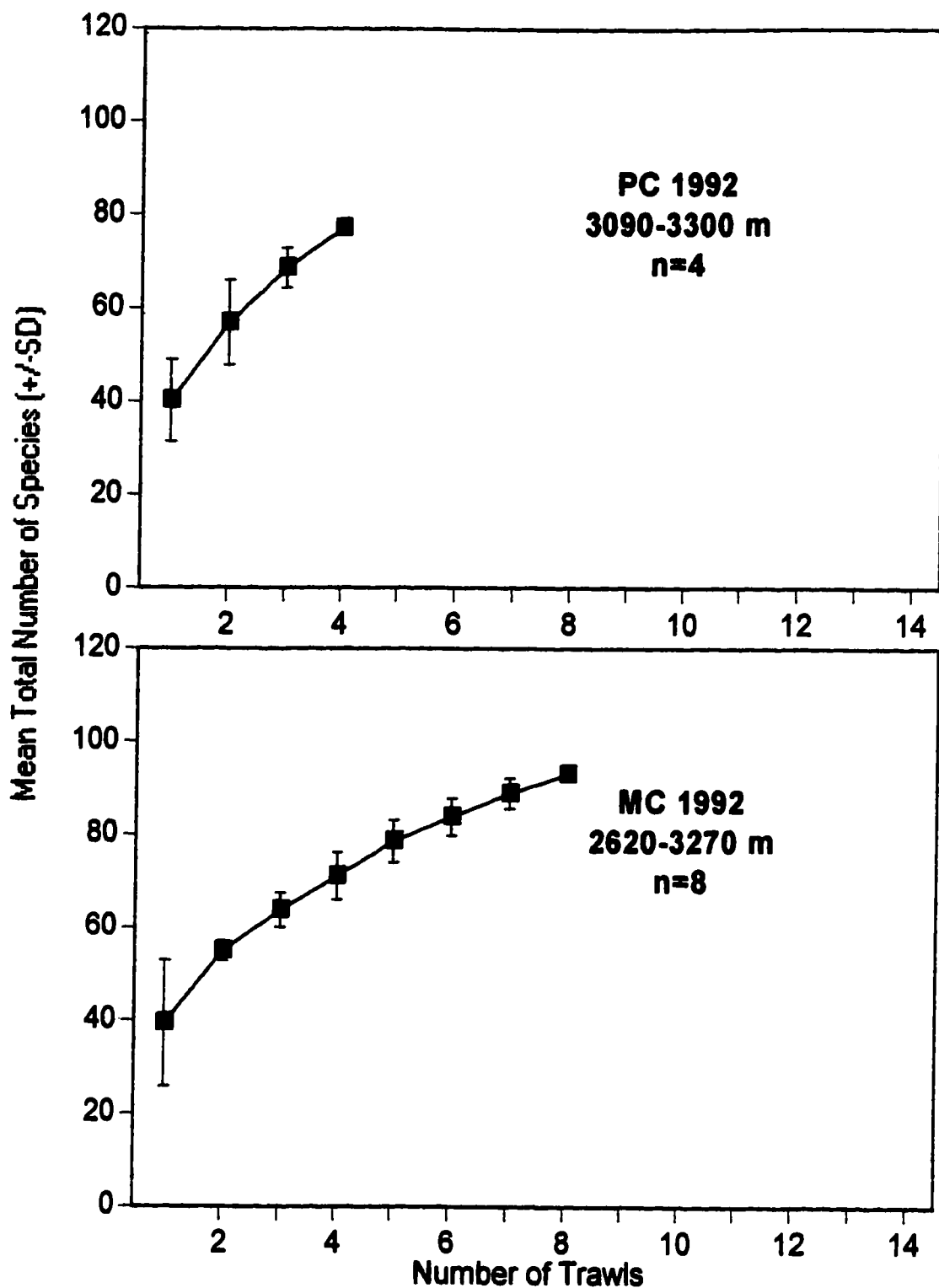


Figure 6. Cumulative species curves for invertebrate megafauna collected with trawls at the Pioneer Canyon and Monterey Canyon sites in 1992. There were 4 trawls at the Pioneer Canyon site and 8 trawls at the Monterey Canyon site. Each value is the mean cumulative number of species +/- the standard deviation for 10 random combination of samples.

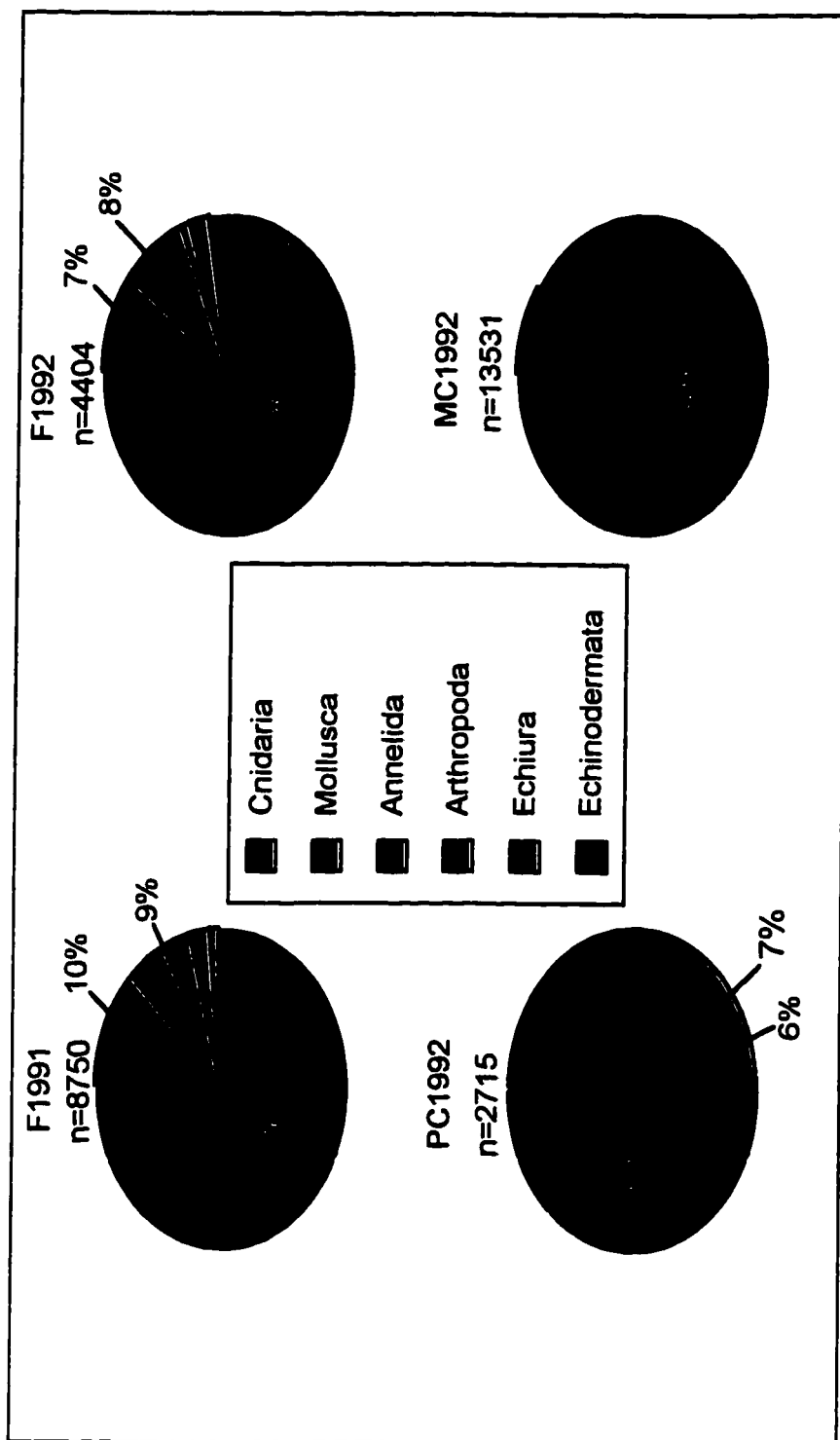


Figure 7. Pie charts showing the relative abundance of the six major invertebrate phyla collected by trawls at the Farallon 1991/1992, Pioneer Canyon, and Monterey Canyon sites.

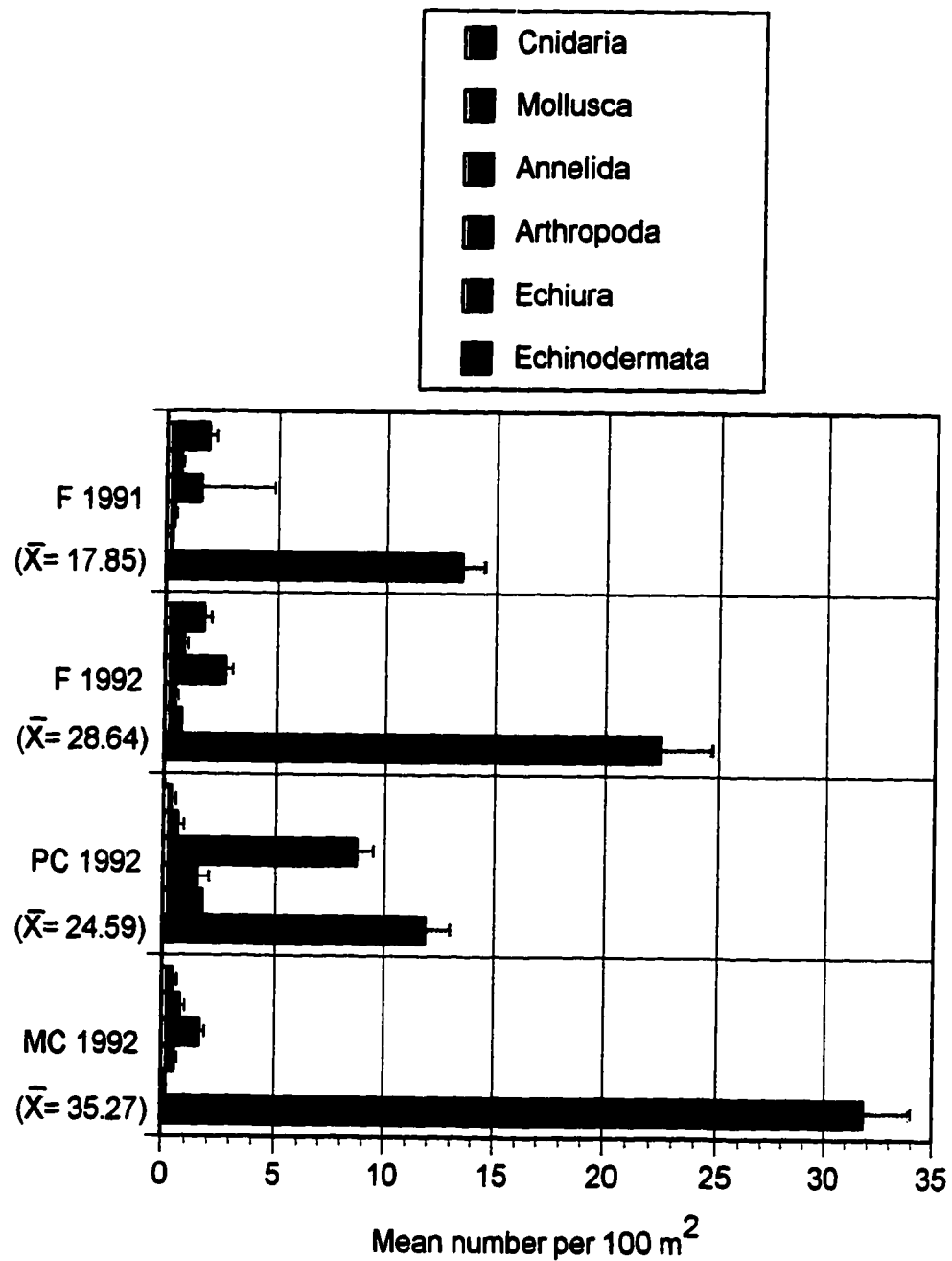


Figure 8. Mean abundance of individuals (by phylum) per 100 m² at the Farallon 1991/1992, Pioneer Canyon, and Monterey Canyon study sites.(+/-SD).

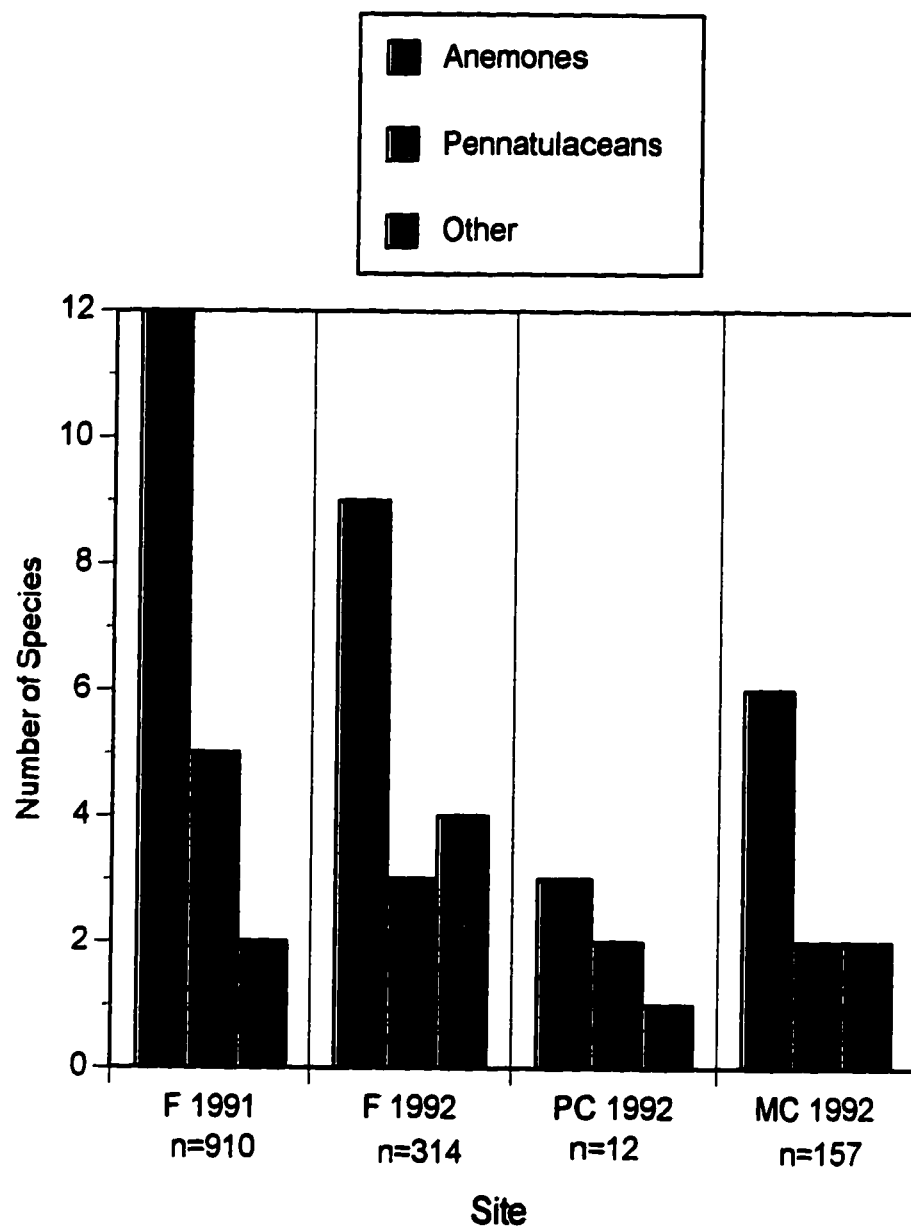


Figure 9. Comparison of the number of cnidaria species by order collected with trawls at the Farallon 1991/1992, Pioneer Canyon, and Monterey Canyon study sites. (Other includes gorgonians, soft corals, etc. Anemones includes actinarians and corallimorpharians.)

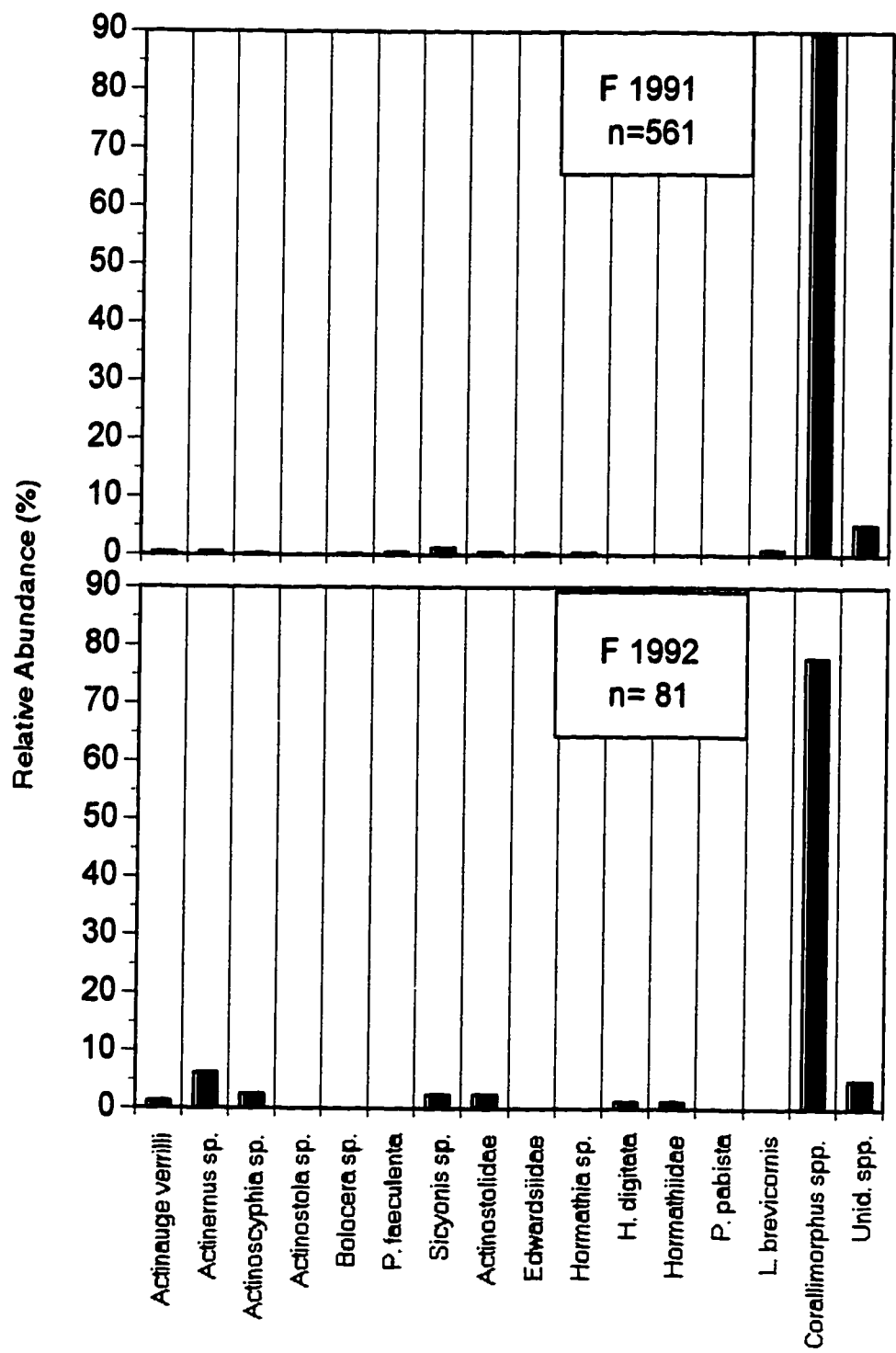


Figure 10a. Comparison of the relative abundances of anemone species/families collected with trawls at the Farallon site in 1991 and 1992.

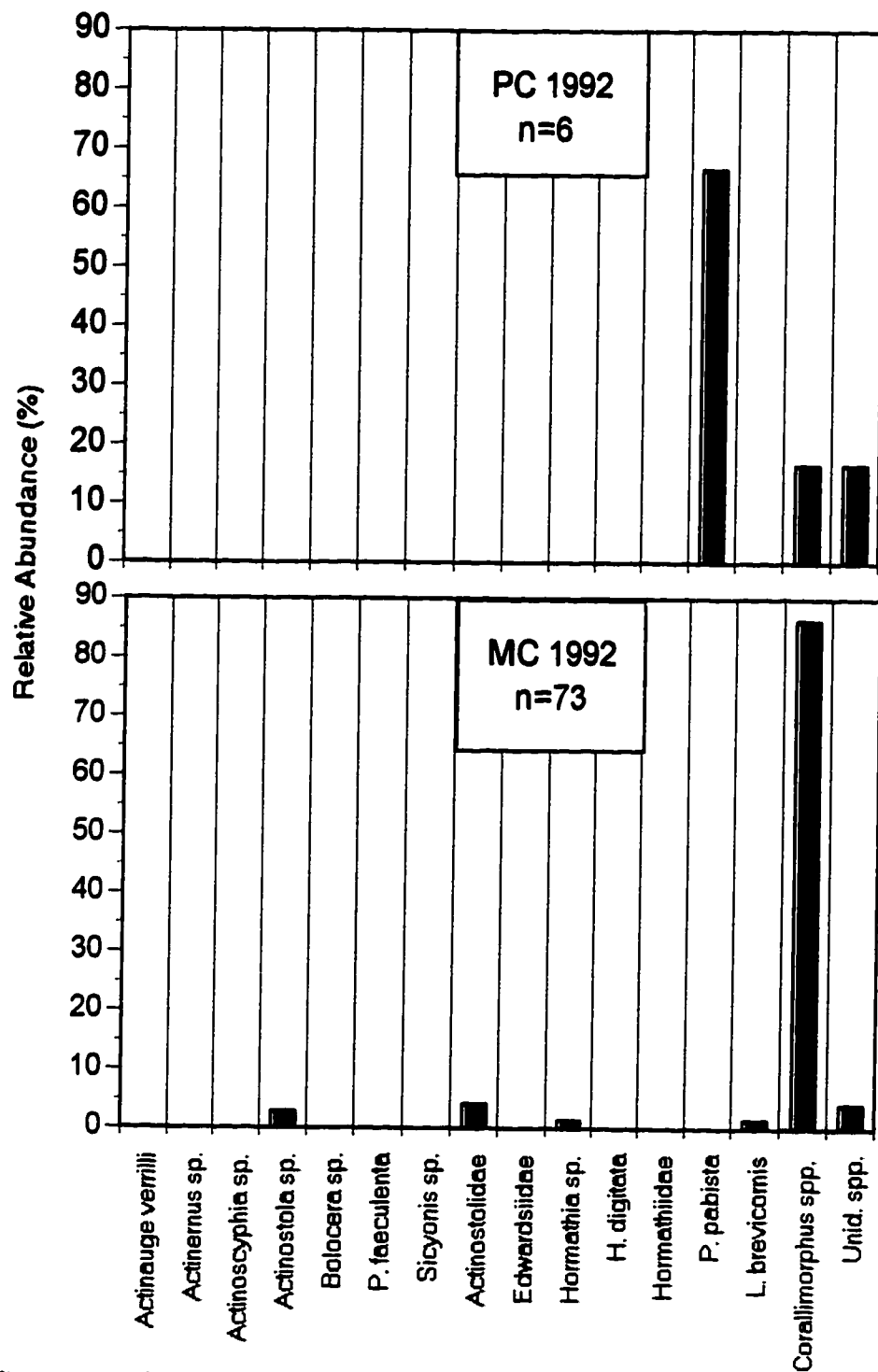


Figure 10b. Comparison of the relative abundances of anemone species/families collected at the Pioneer Canyon and Monterey Canyon sites in 1992.

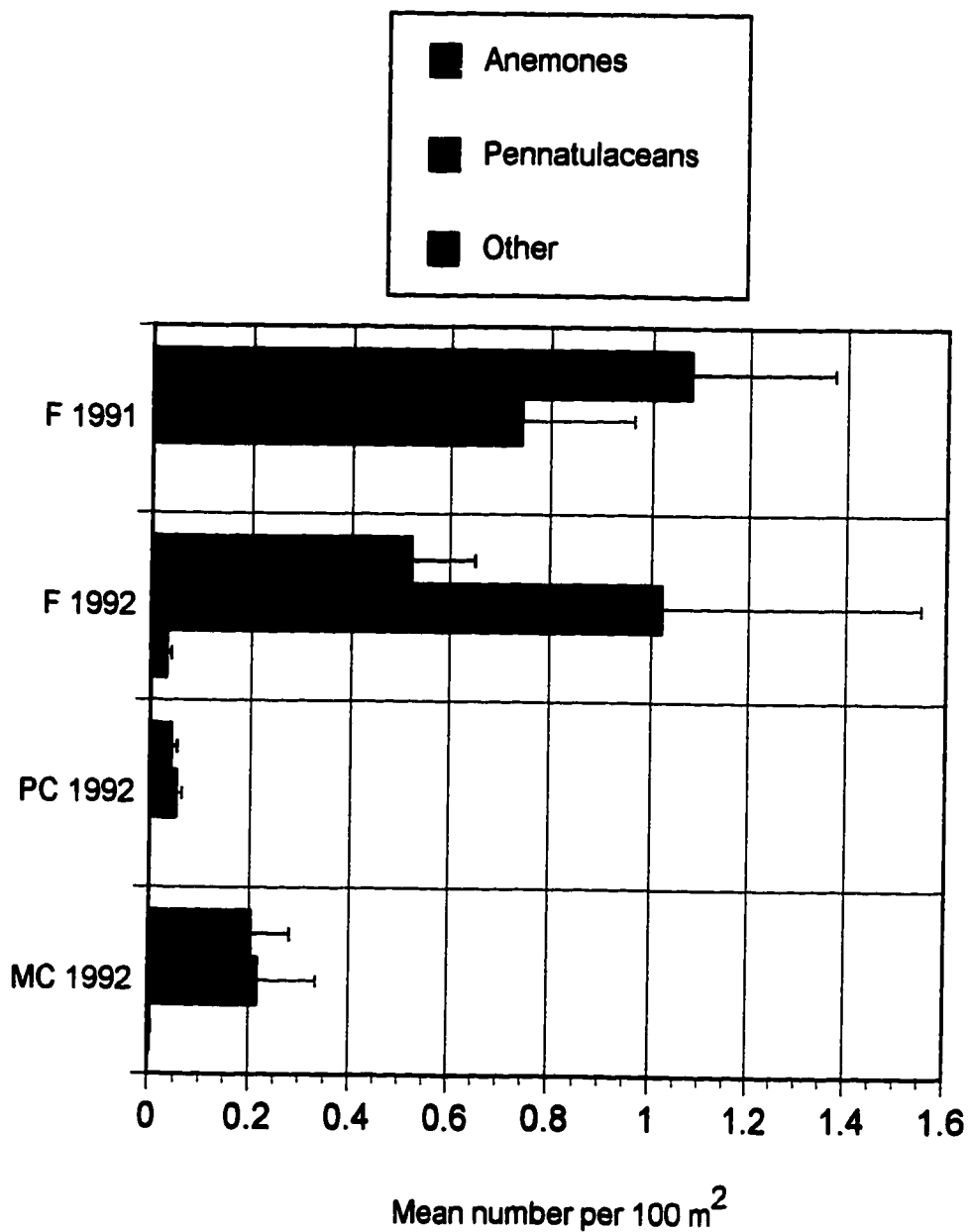


Figure 11. Mean abundance of cnidarians (by order) per 100 m² at the Farallon 1991/1992, Pioneer Canyon, and Monterey Canyon study sites (+/- SD). (Other includes gorgonians, corals, etc. Anemones include actinarians and corallimorpharians .)

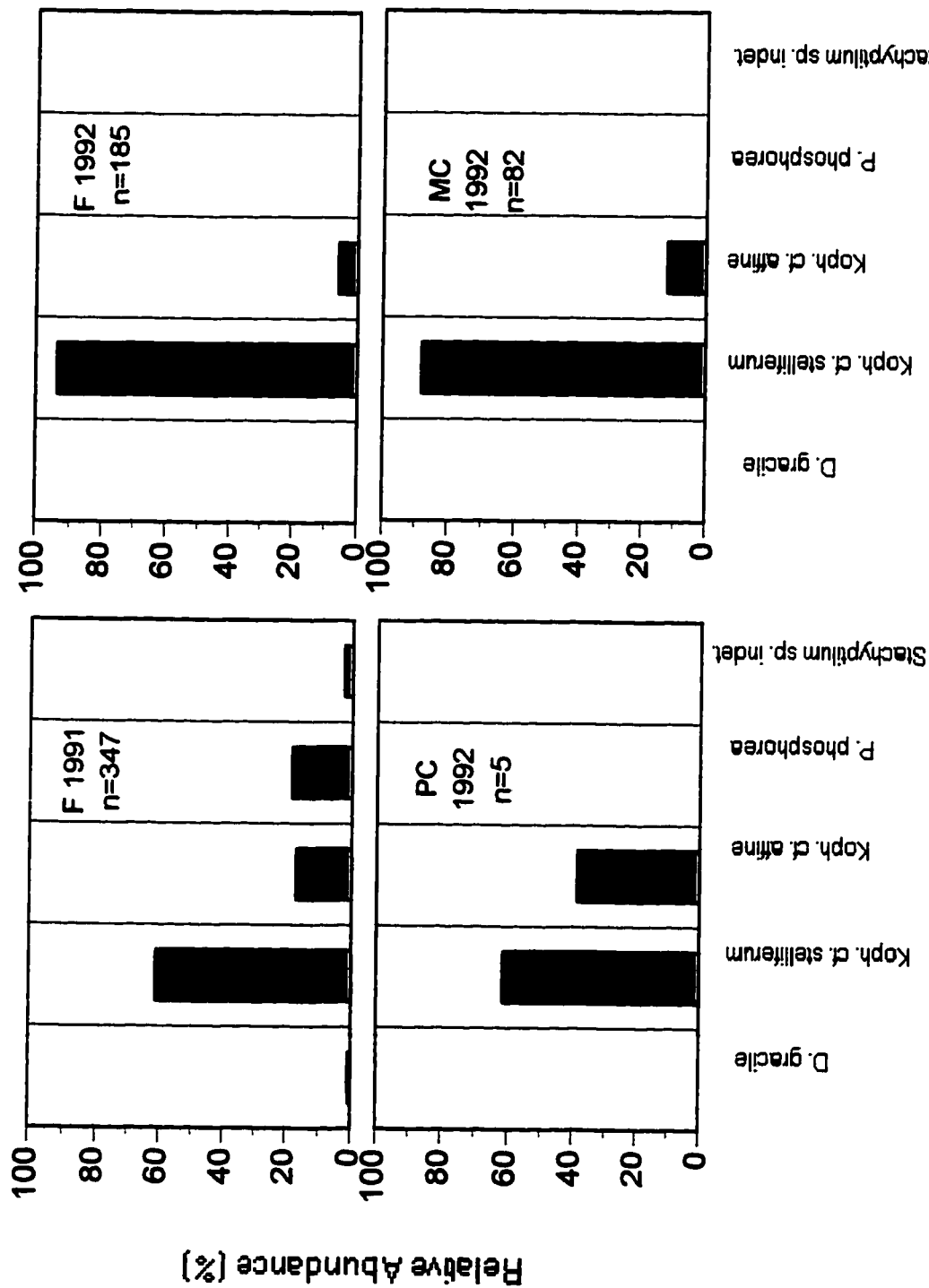


Figure 12. Comparison of the relative abundances of sea pen species collected with trawls at the Farallon 1991/1992, Pioneer Canyon, and Monterey Canyon sites.

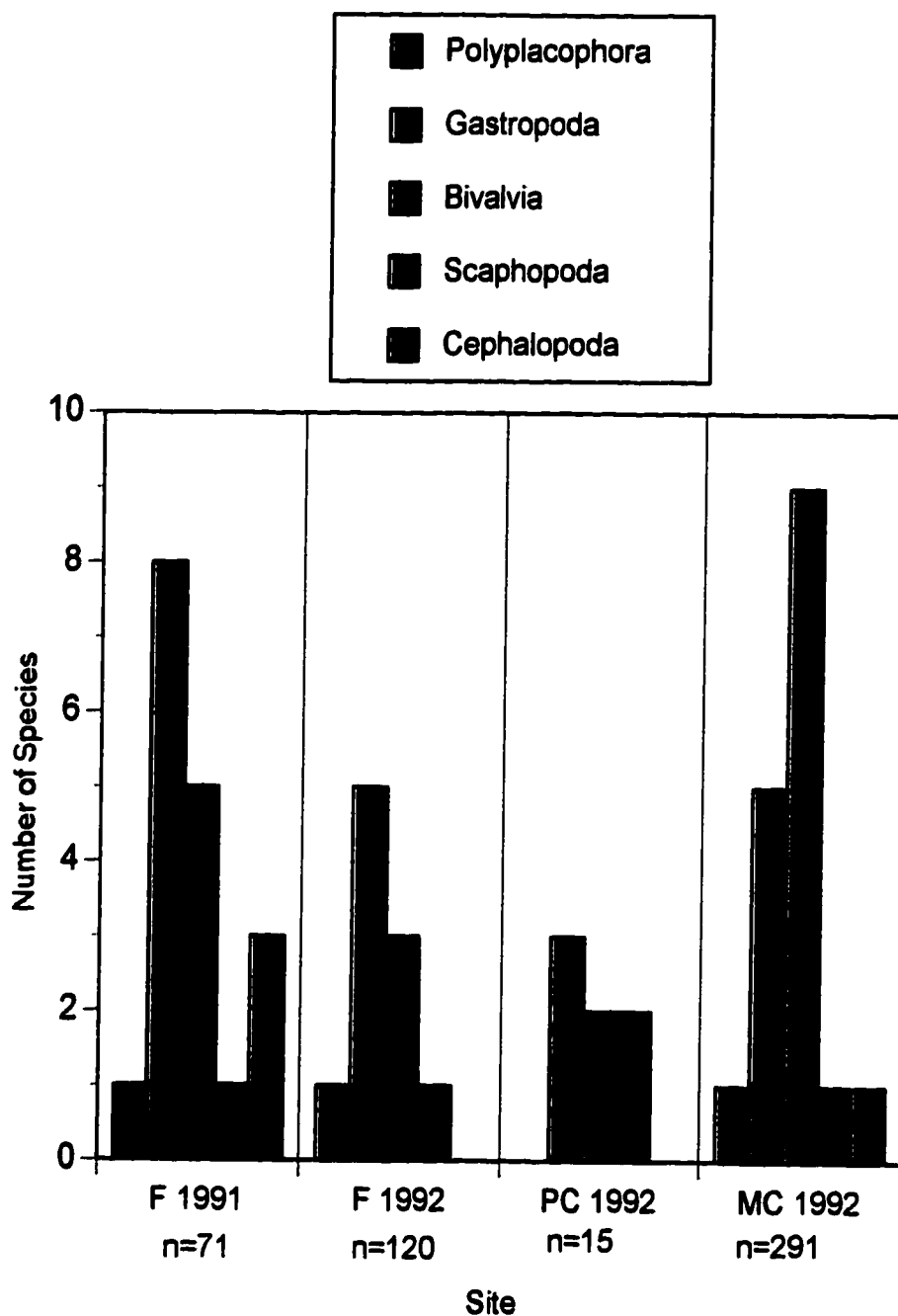


Figure 13. Comparison of the number of species of molluscs by class collected with trawls at the Farallon 1991/1992, Pioneer Canyon, and Monterey Canyon sites.

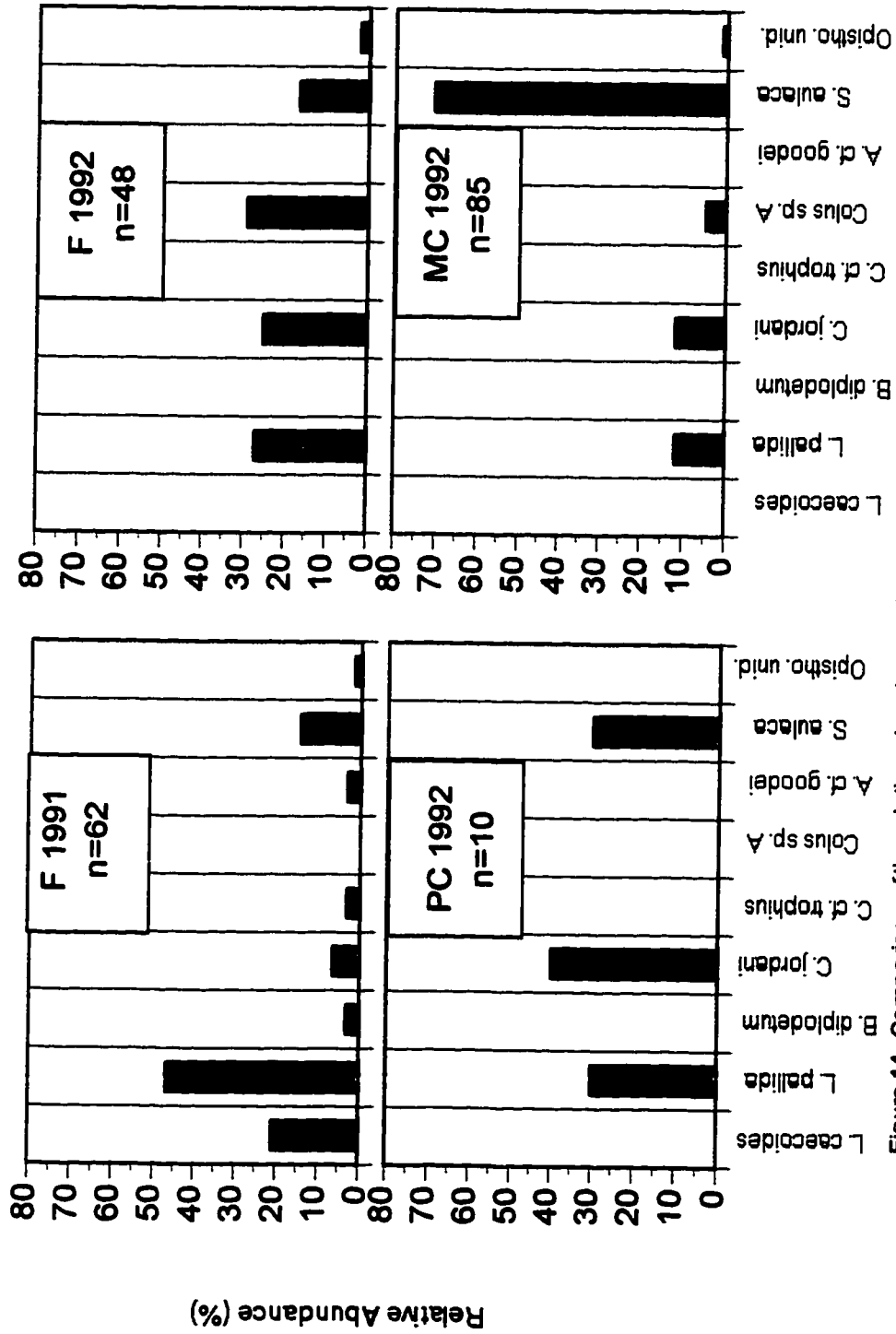


Figure 14. Comparison of the relative abundance of gastropod species collected with trawls at the Farallon 1991/1992, Pioneer Canyon, and Monterey Canyon sites.

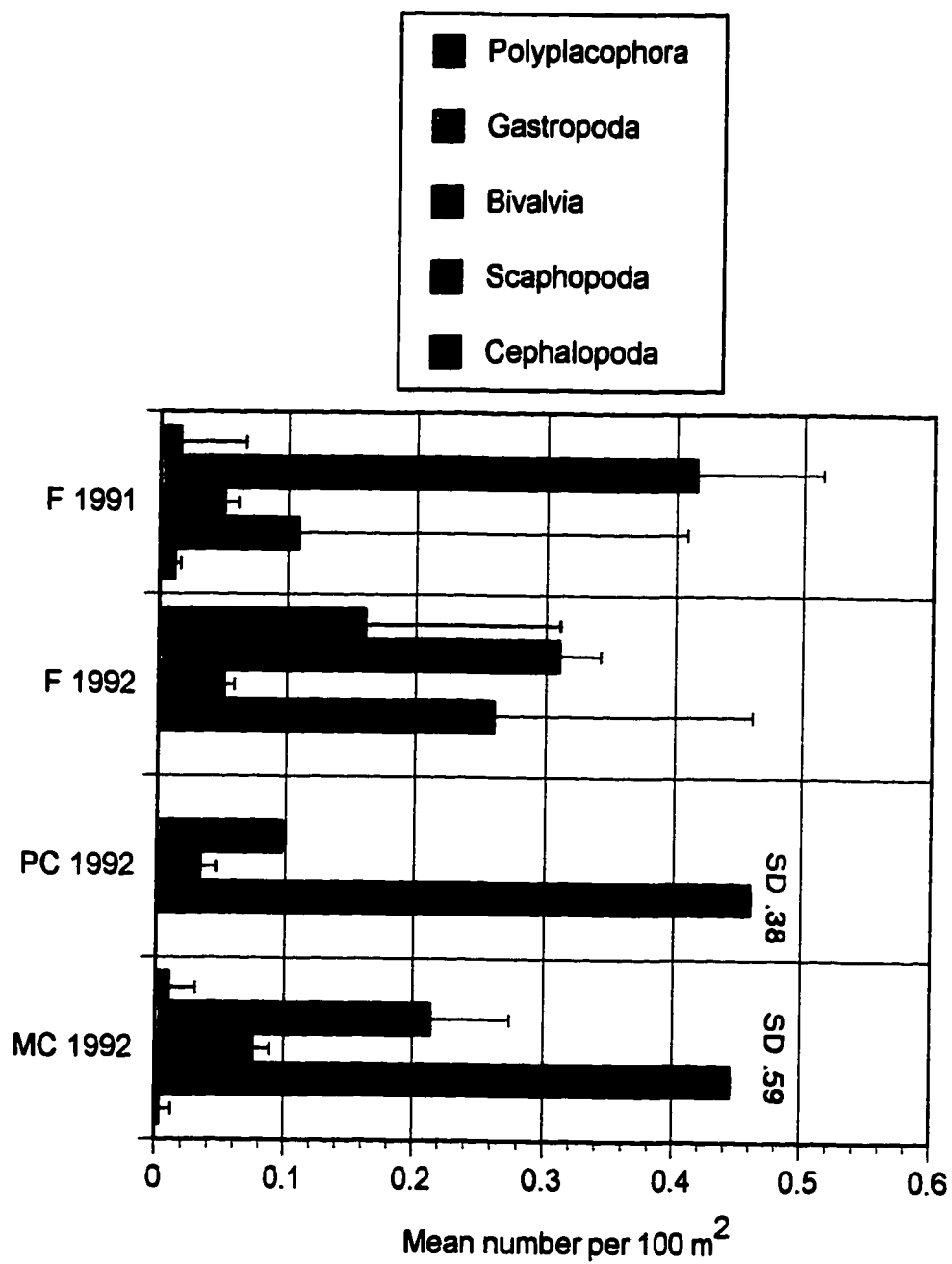


Figure 15. Mean abundance of molluscs (by class) per 100 m² at the Farallon 1991/1992, Pioneer Canyon, and Monterey Canyon study sites (+/-SD).

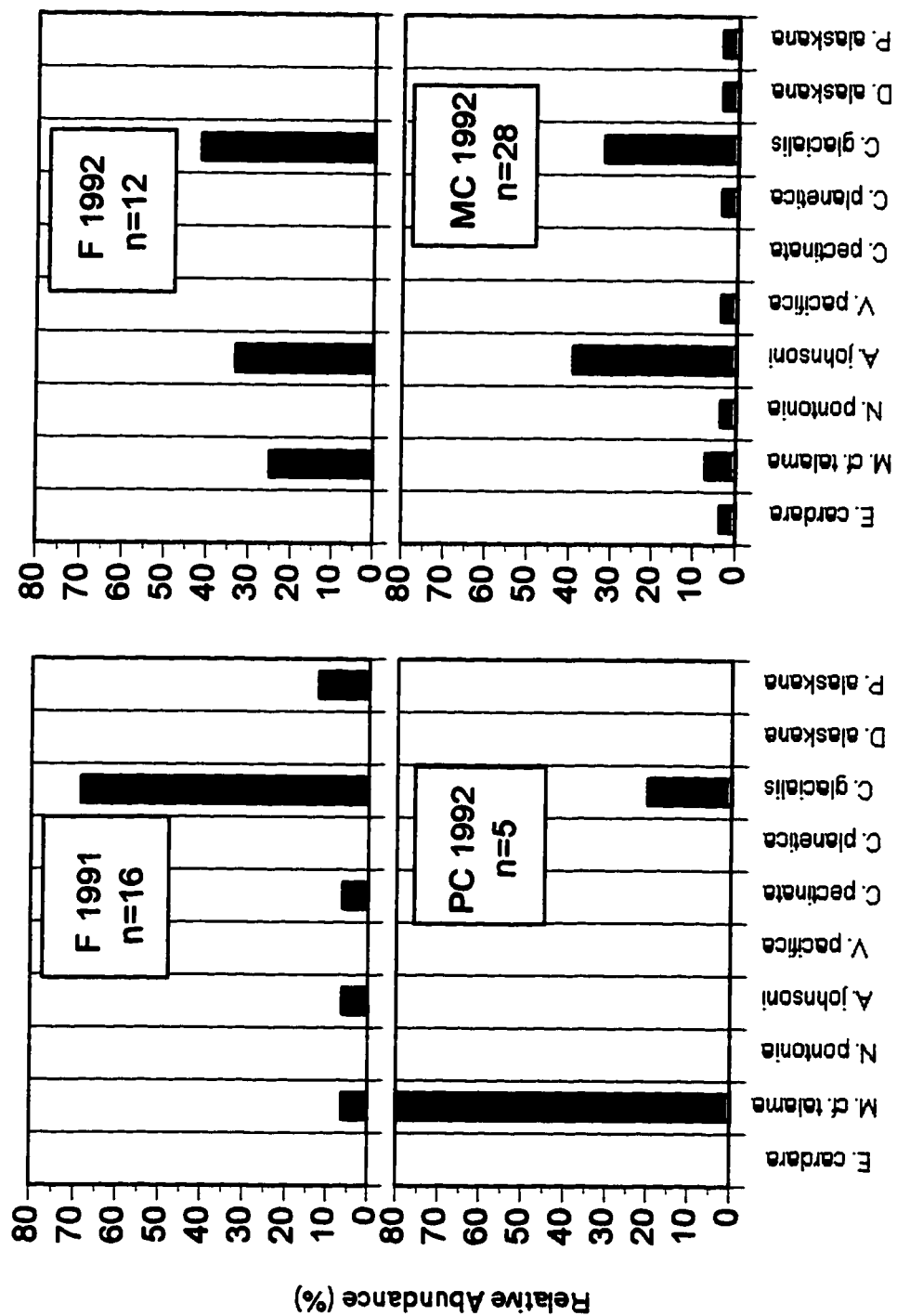


Figure 16. Comparison of the relative abundance of bivalve species collected with trawls at the Farallon 1991/1992, Pioneer Canyon, and Monterey Canyon sites.

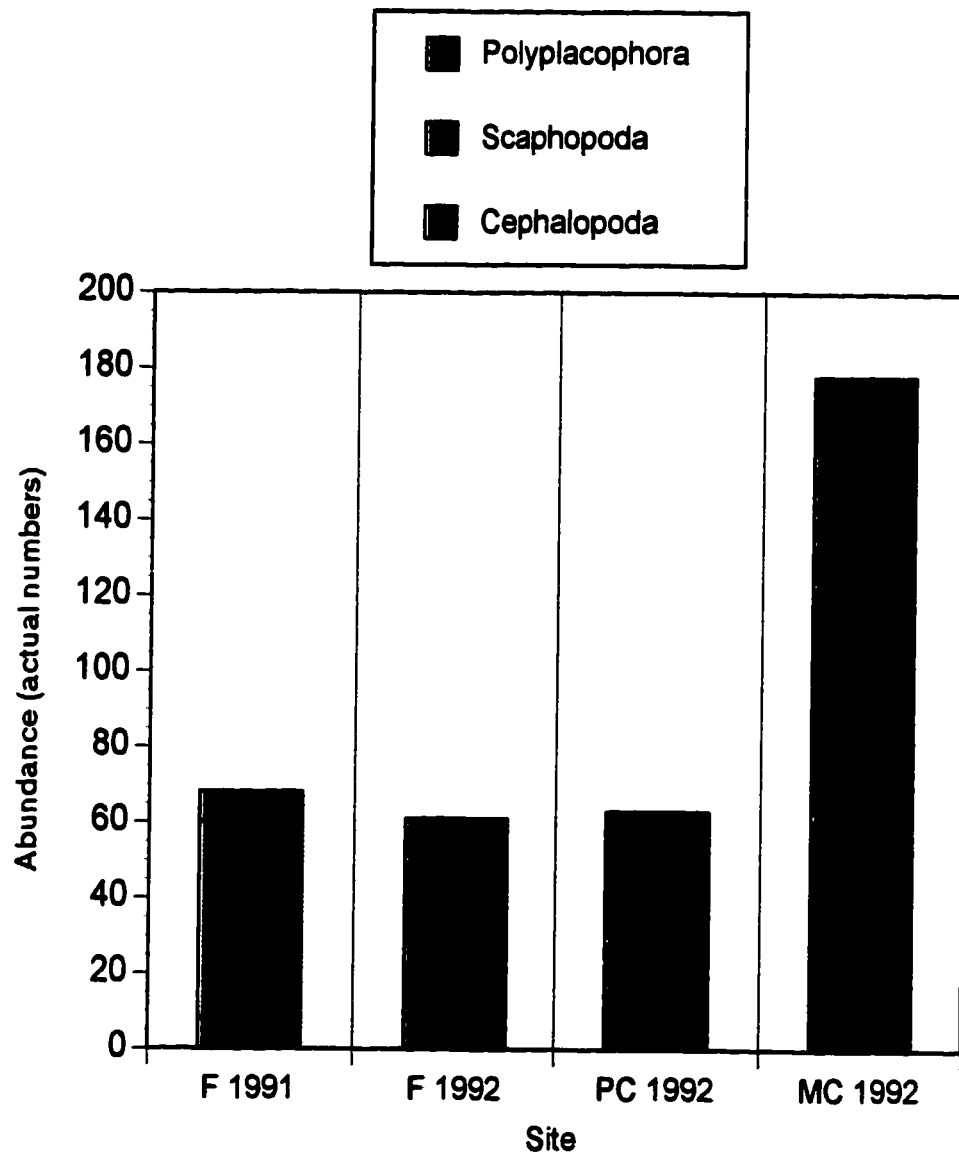


Figure 17. Comparison of the actual abundance of polyplacophorans (?*Leptochiton alveolus*), scaphopods (*Fissidentalium megathyrus*), and Cephalopods (*Benthoctopus* sp., *Graneledone pacifica*, and *Vampyroteuthis infernalis*) collected with trawls at the Farallon 1991/1992, Pioneer Canyon, and Monterey Canyon sites.

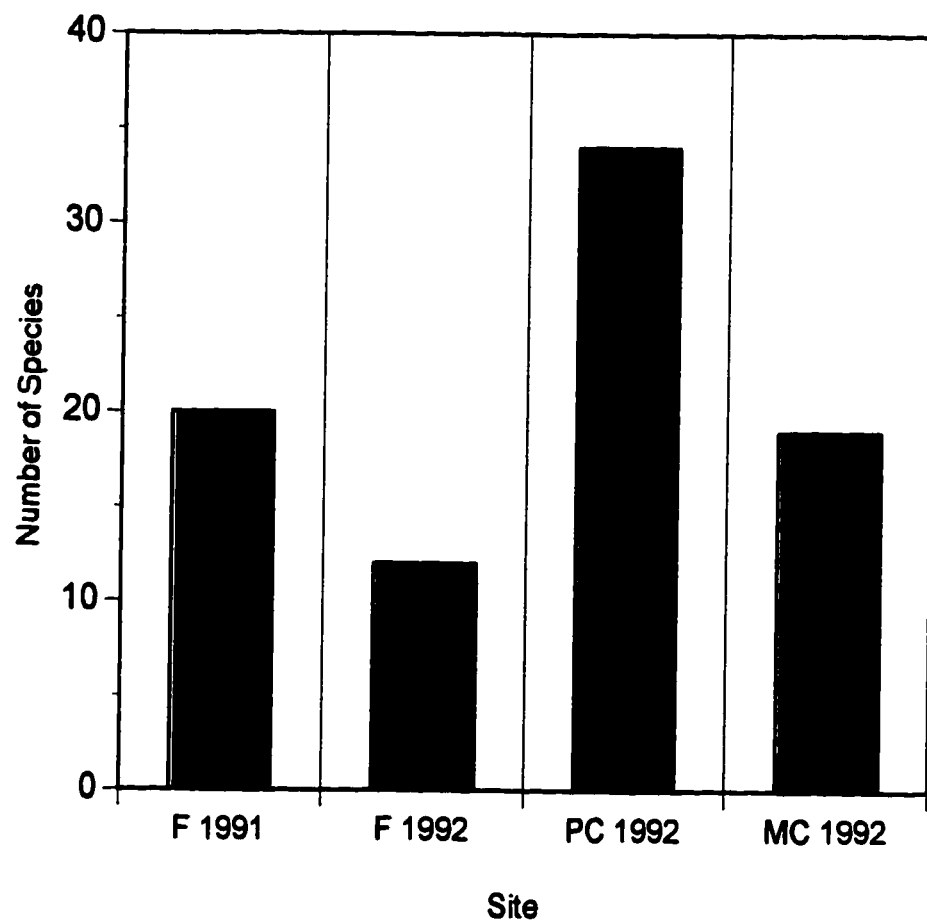


Figure 18. Comparison of the number of polychaete species/taxa collected with trawls at the Farallon 1991/1992, Pioneer Canyon, and Monterey Canyon sites.

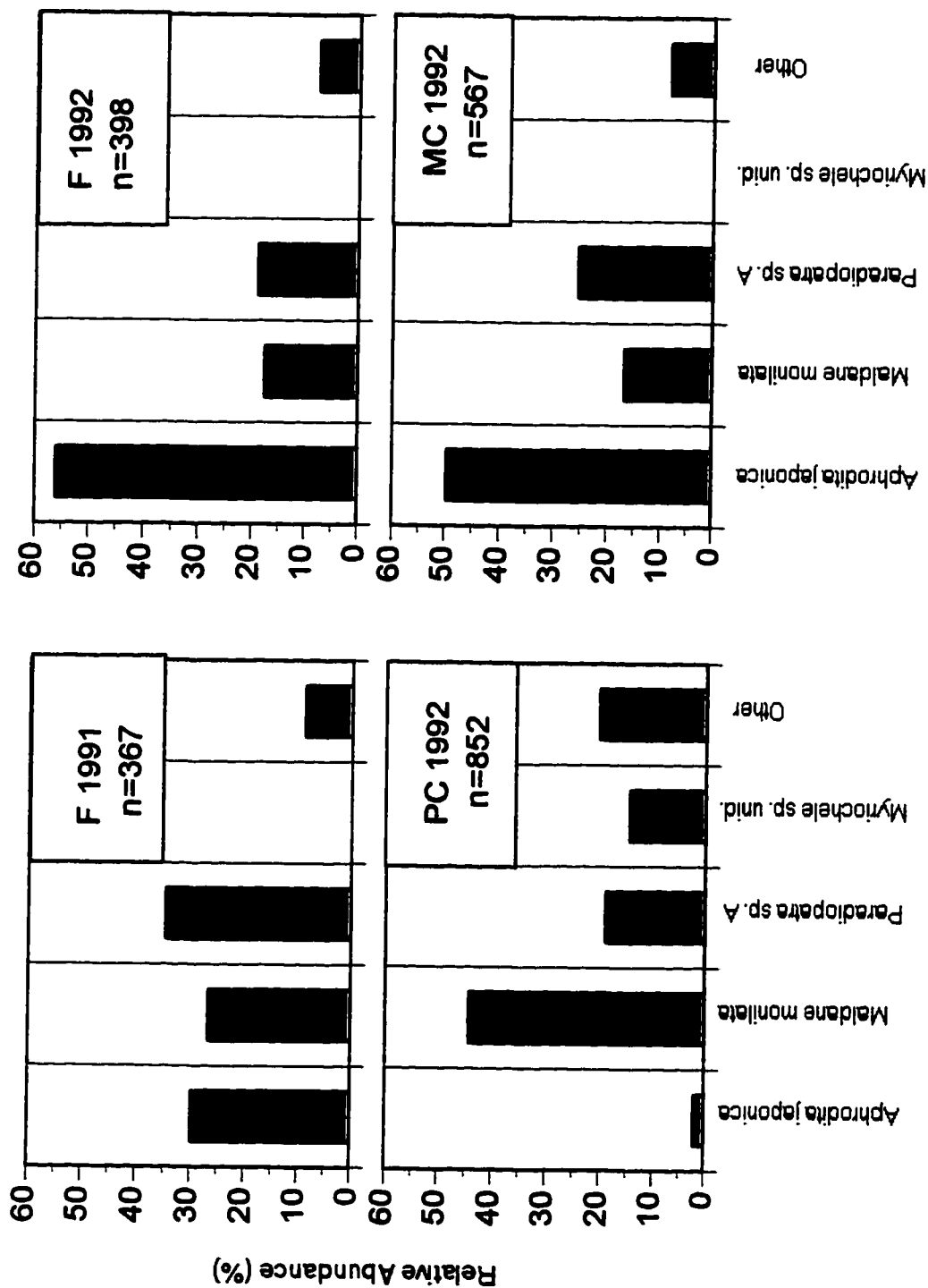


Figure 19. Comparison of the relative abundance of the most common polychaete species collected with trawls at the Farallon 1991/1992, Pioneer Canyon, and Monterey Canyon sites.

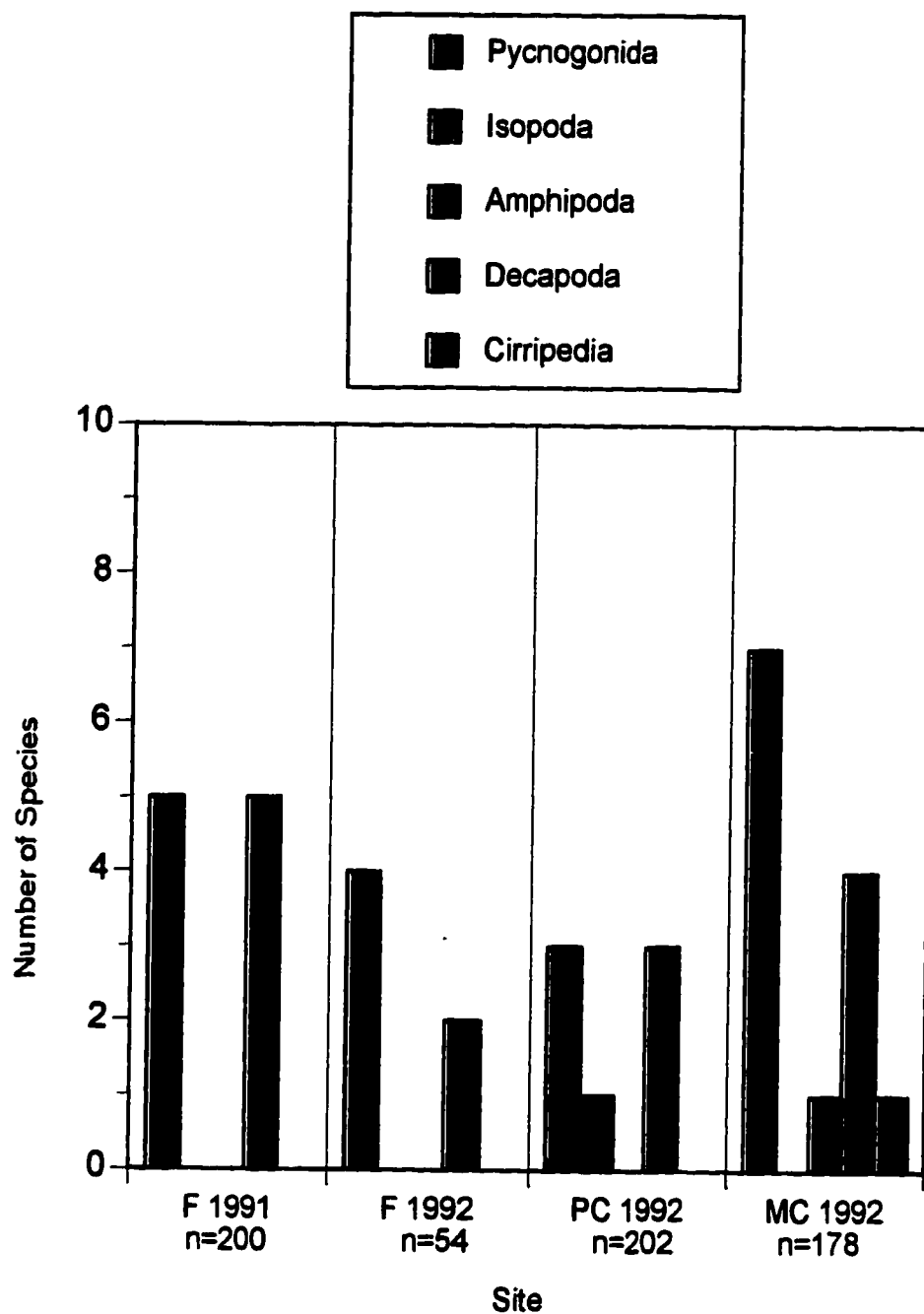


Figure 20. Comparison of the number of arthropod species by group as collected with trawls at the Farallon 1991/1992, Pioneer Canyon, and Monterey Canyon study sites (cirripedia is in larval form only).

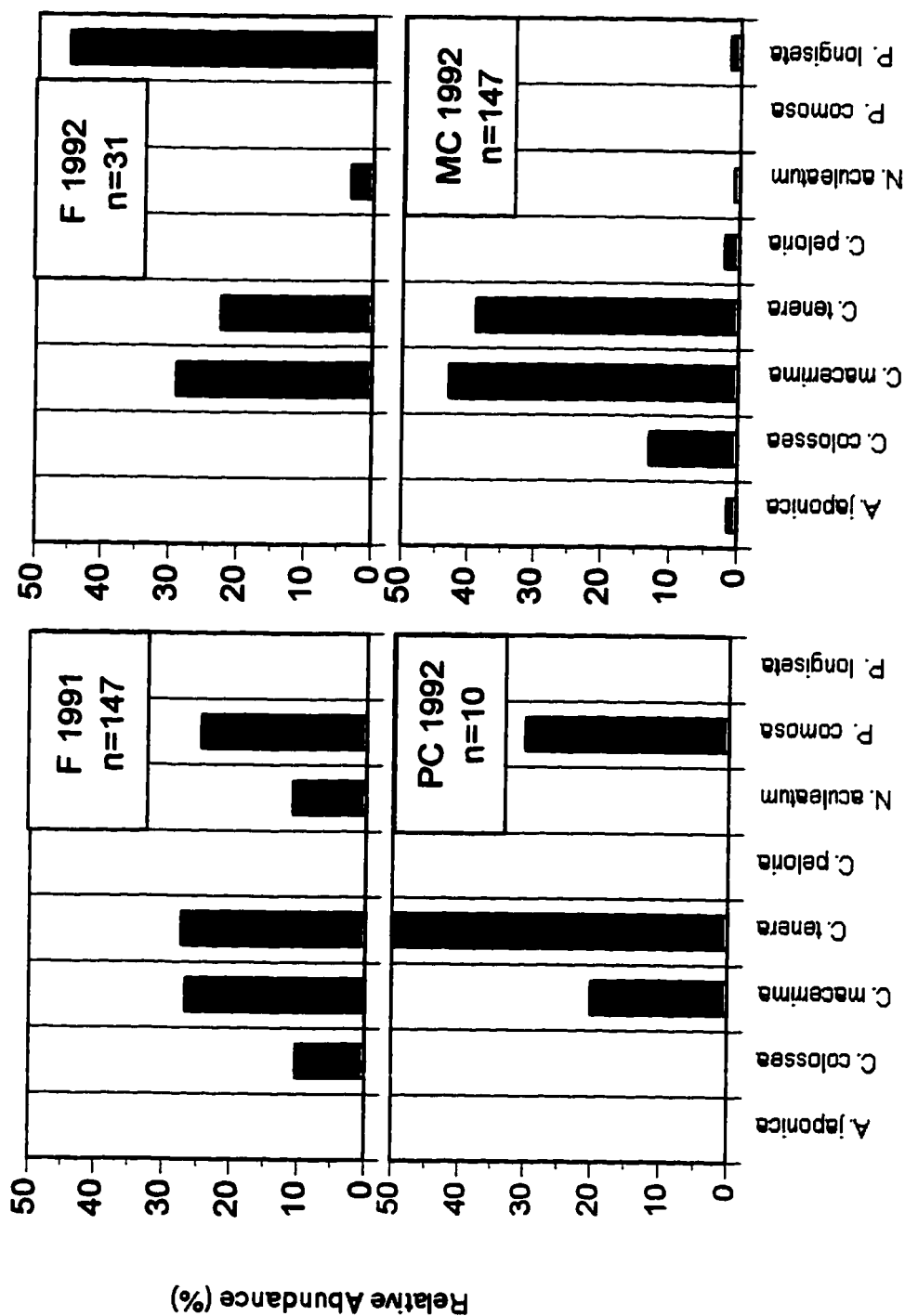


Figure 21. Comparison of the relative abundances of pycnogonid species collected with trawls at the Farallon 1991/1992, Pioneer Canyon, and Monterey Canyon study sites.

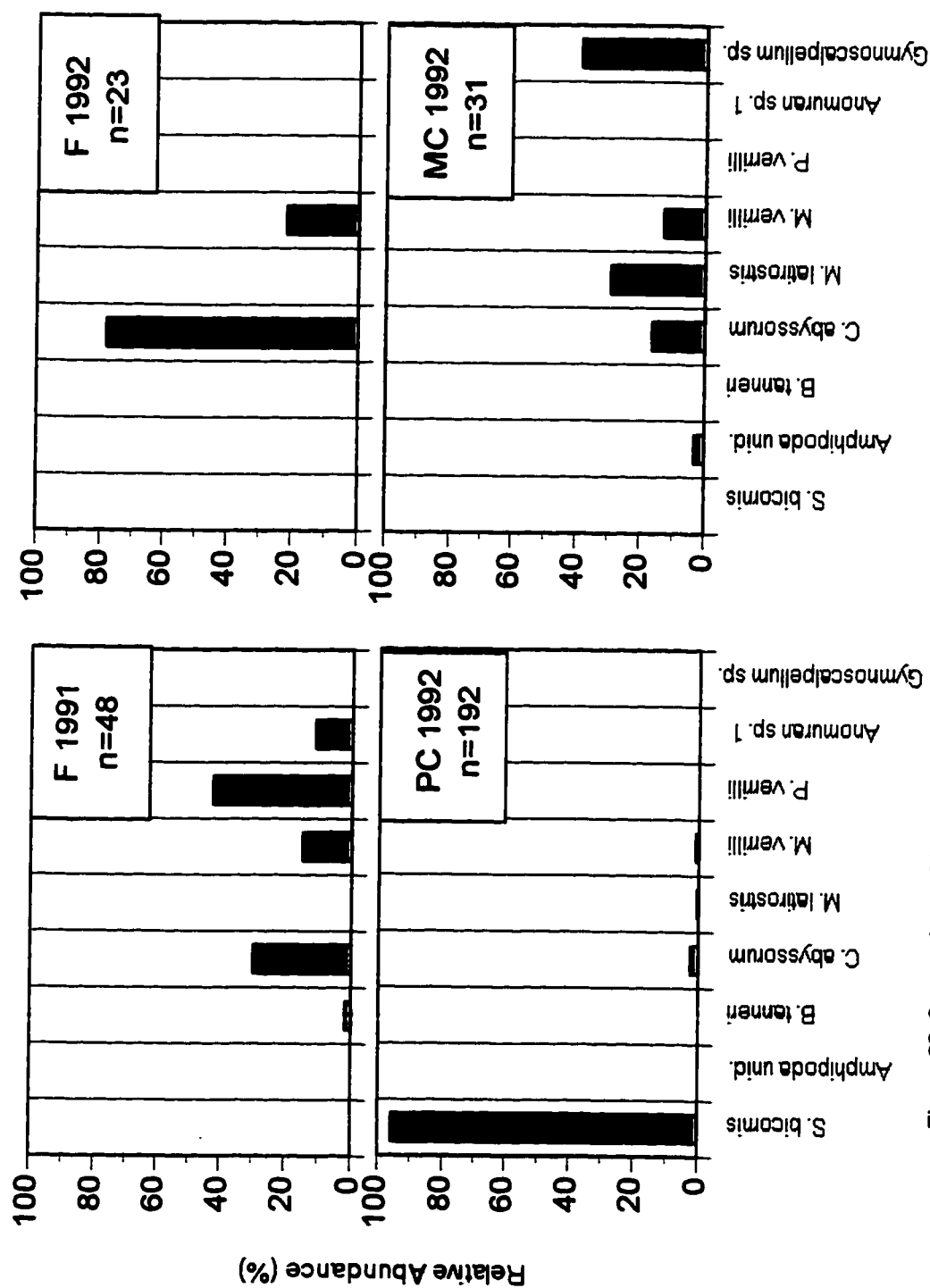


Figure 22. Comparison of the relative abundance of crustacea species collected with trawls at the Farallon 1991/1992, Pioneer Canyon, and Monterey Canyon study sites.

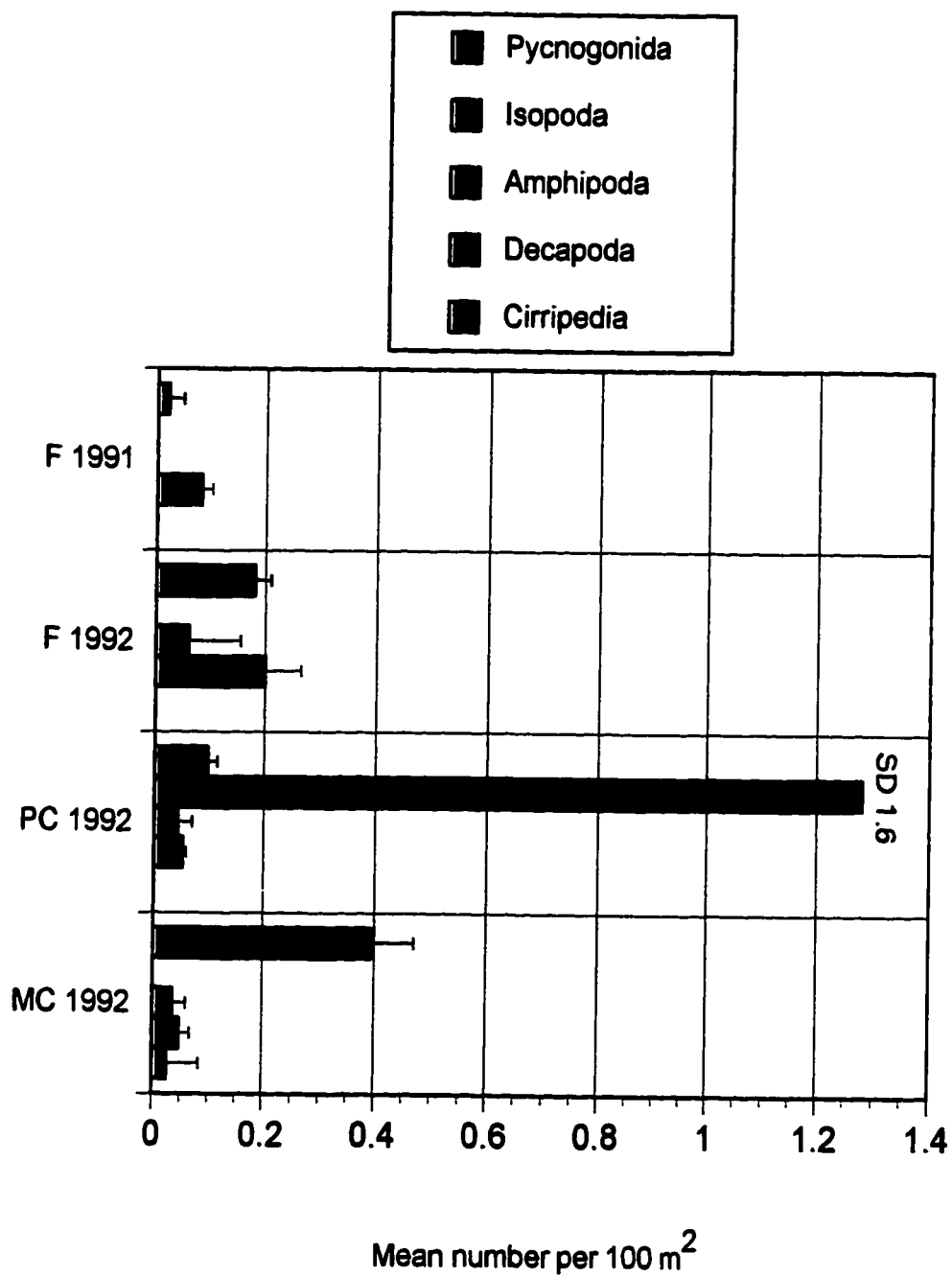


Figure 23. Mean abundance of arthropods (by group) per 100 m² at the Farallon 1991/1992, Pioneer Canyon, and Monterey Canyon study sites (+/-SD). (Cirripedia is in larval form only).

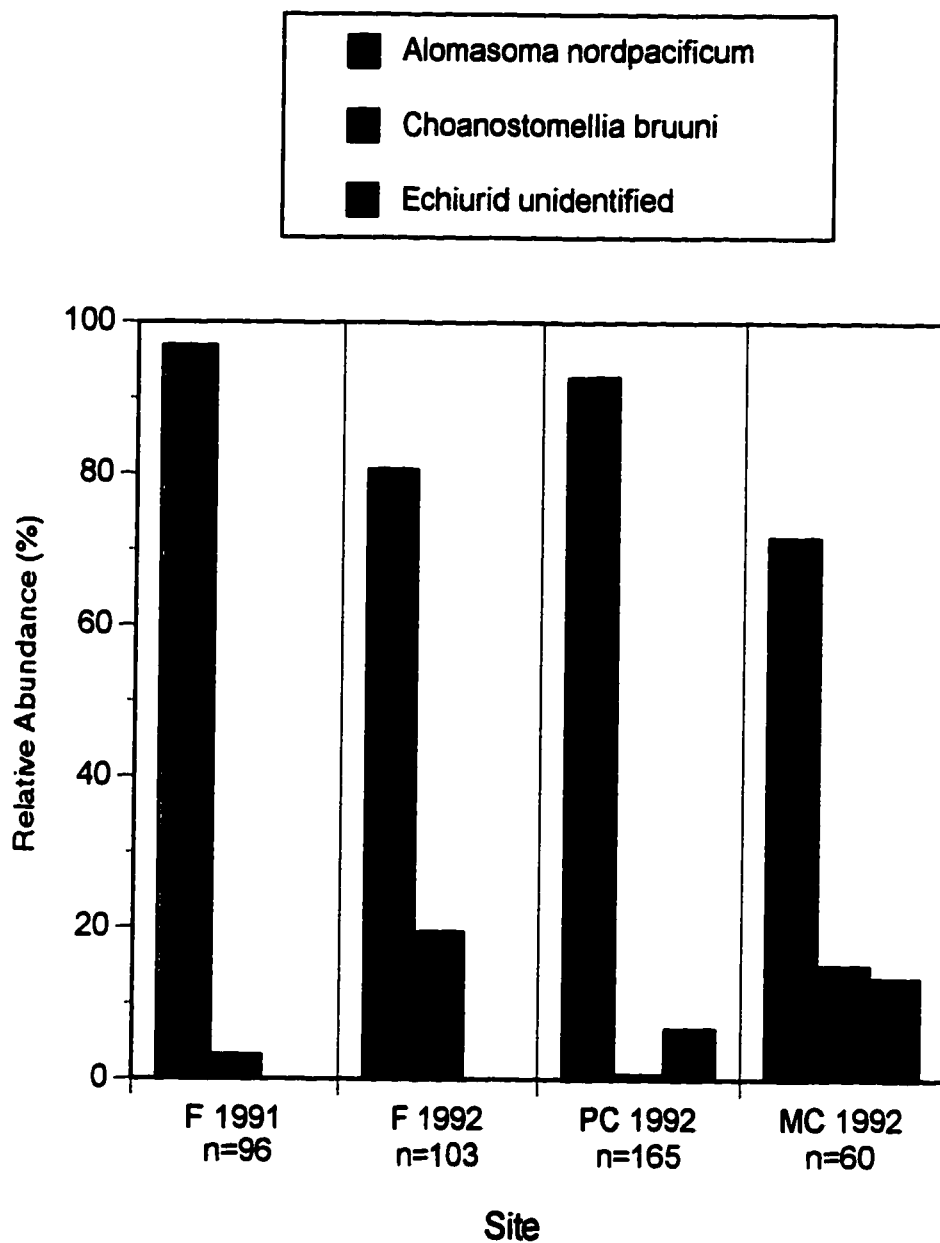


Figure 24. Comparison of the relative abundance of echiura species collected with trawls at the Farallon 1991/1992, Pioneer Canyon, and Monterey Canyon sites.

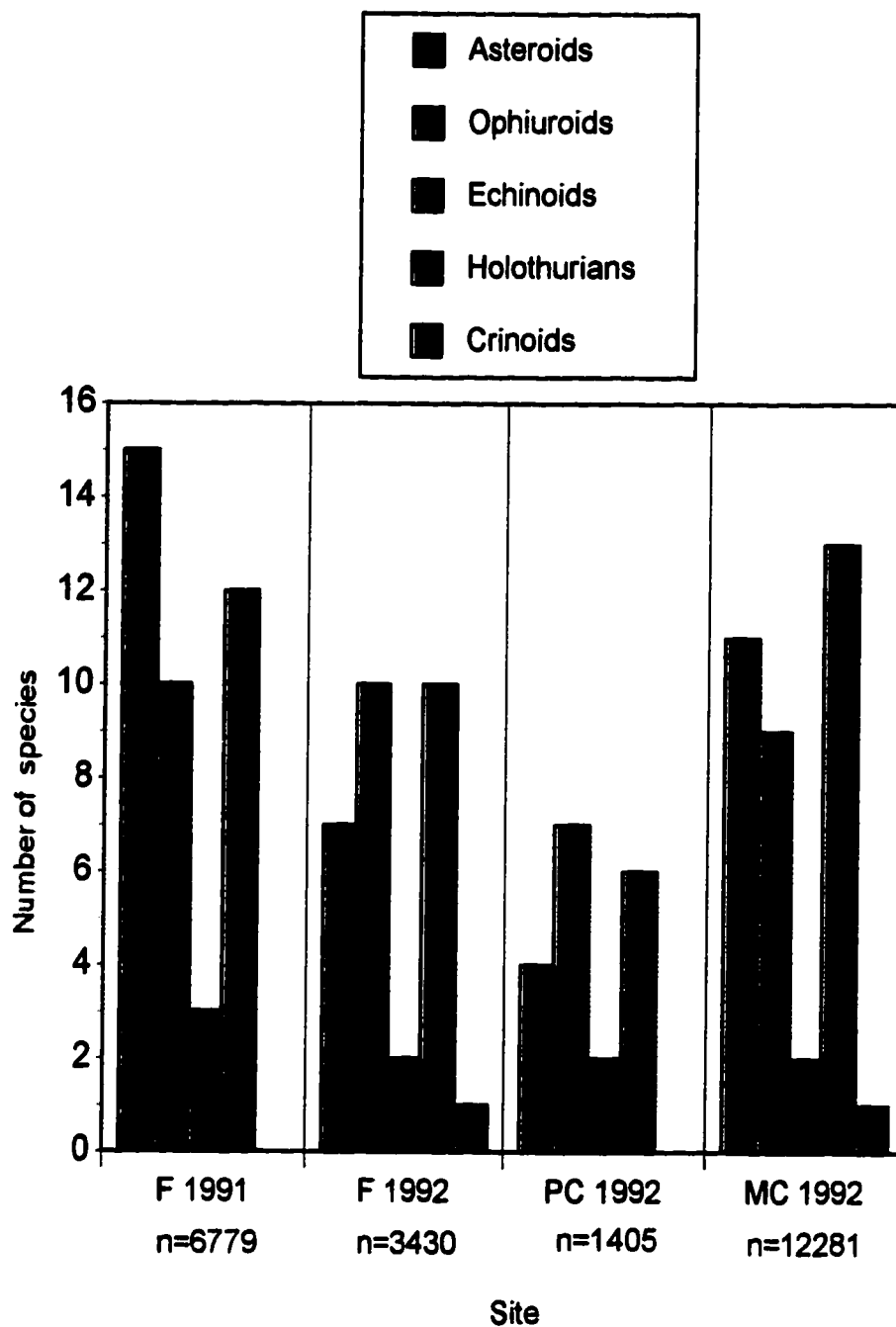


Figure 25. Comparison of the number of echinoderm species by class as collected with trawls at the Farallon 1991/1992, Pioneer Canyon, and Monterey Canyon study sites.

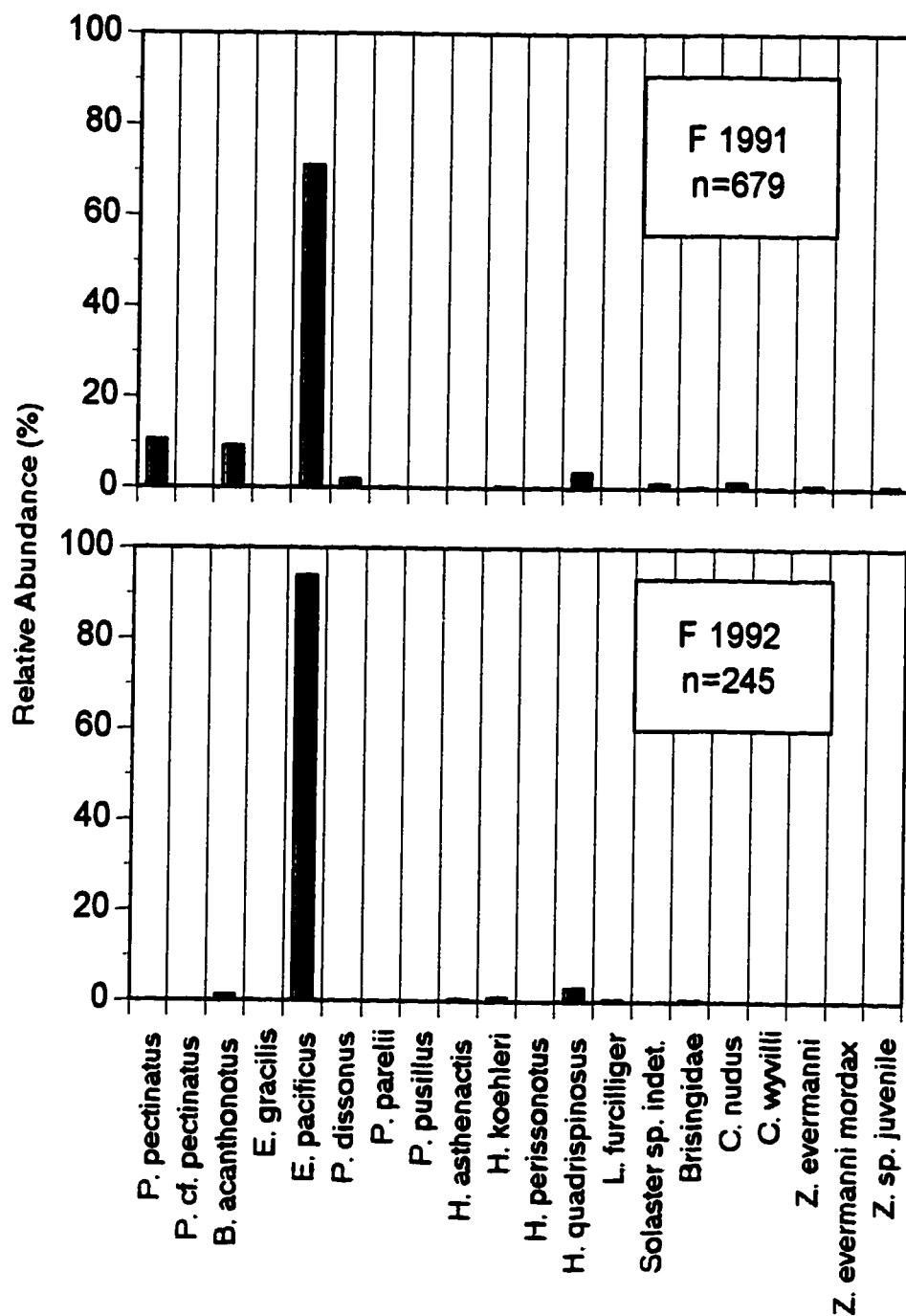


Figure 26. Comparison of the relative abundance of asteroid species collected with trawls at the Farallon site, 1991 and 1992.

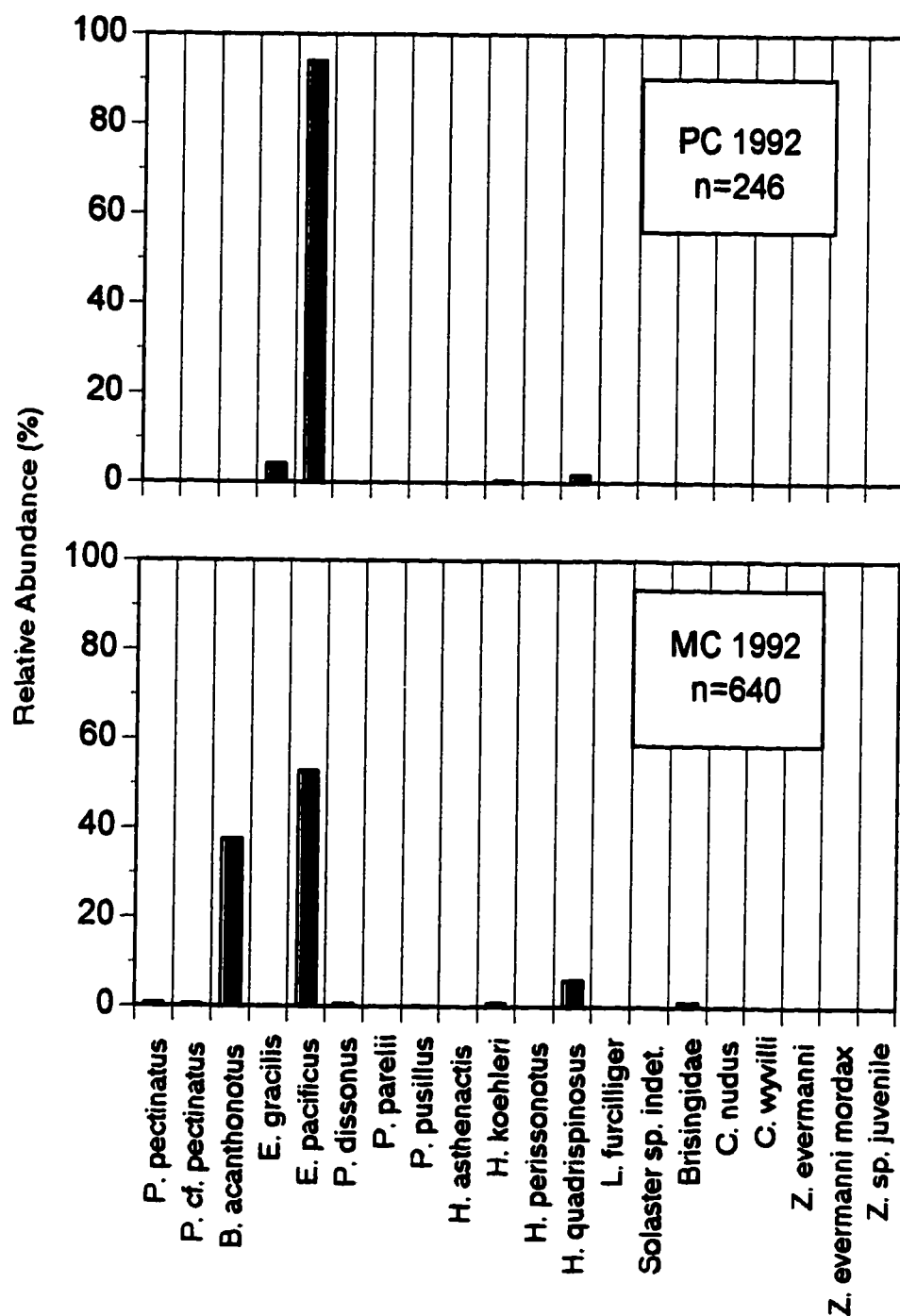


Figure 27. Comparison of the relative abundance of asteroid species collected with trawls at the Pioneer Canyon and Monterey Canyon sites in 1992.

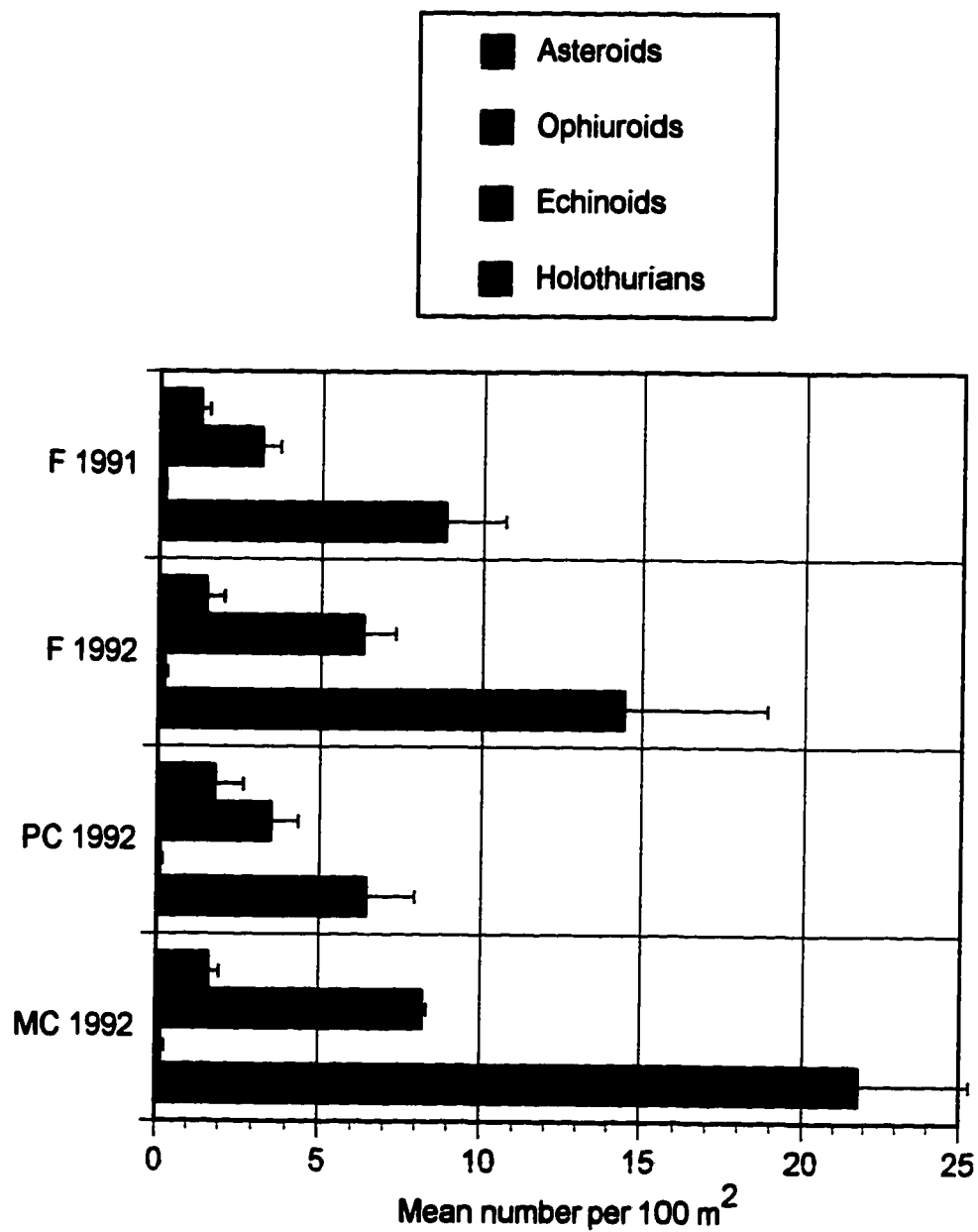


Figure 28. Mean abundance of echinoderms (by class) per 100 m² at the Farallon 1991/1992, Pioneer Canyon, and Monterey Canyon study sites (+/-SD). (Crinoids are excluded because of extremely low densities.)

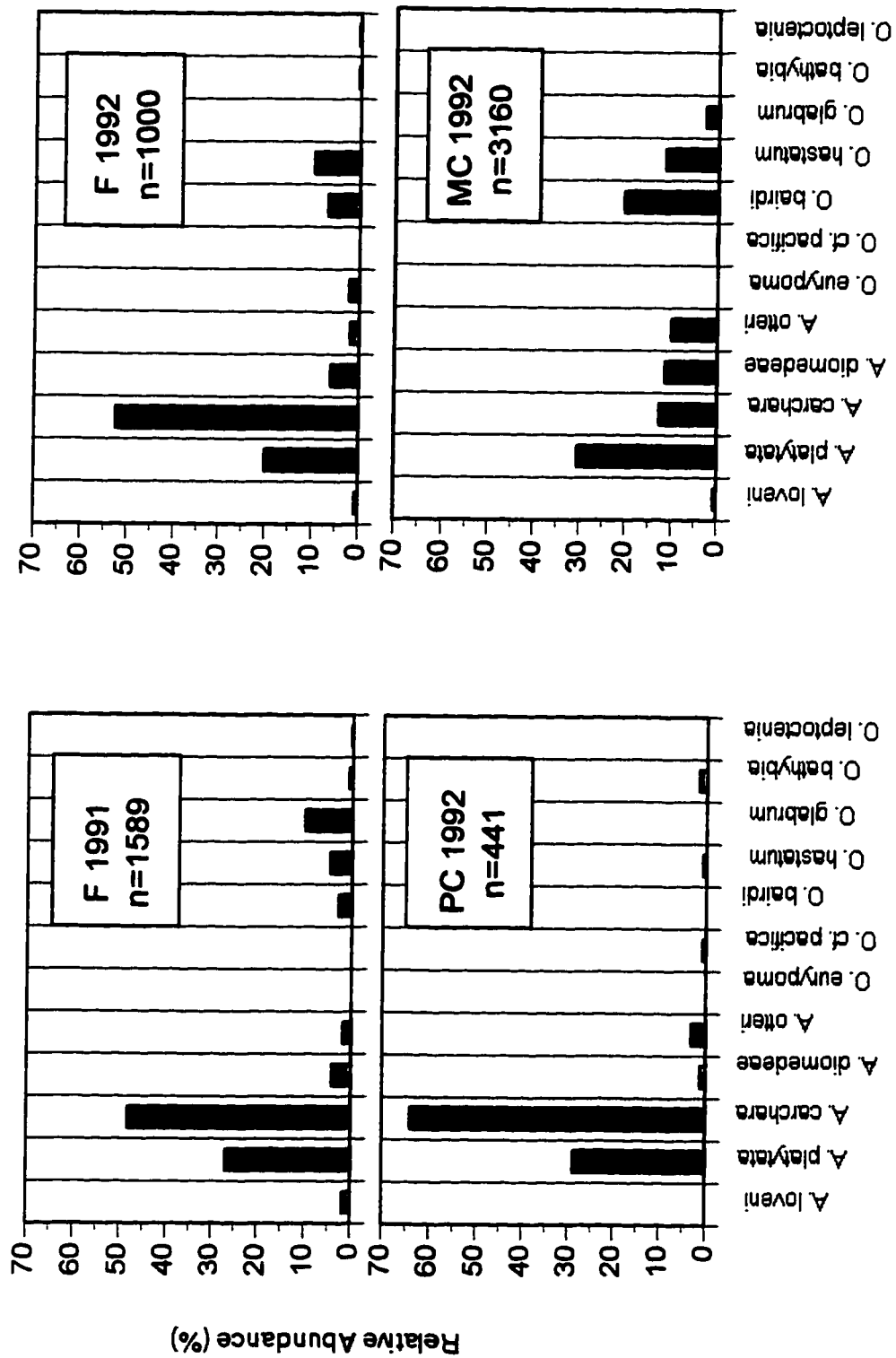


Figure 29. Comparison of the relative abundances of ophiuroid species collected with trawls at the Farallon 1991/1992, Pioneer Canyon, and Monterey Canyon sites.

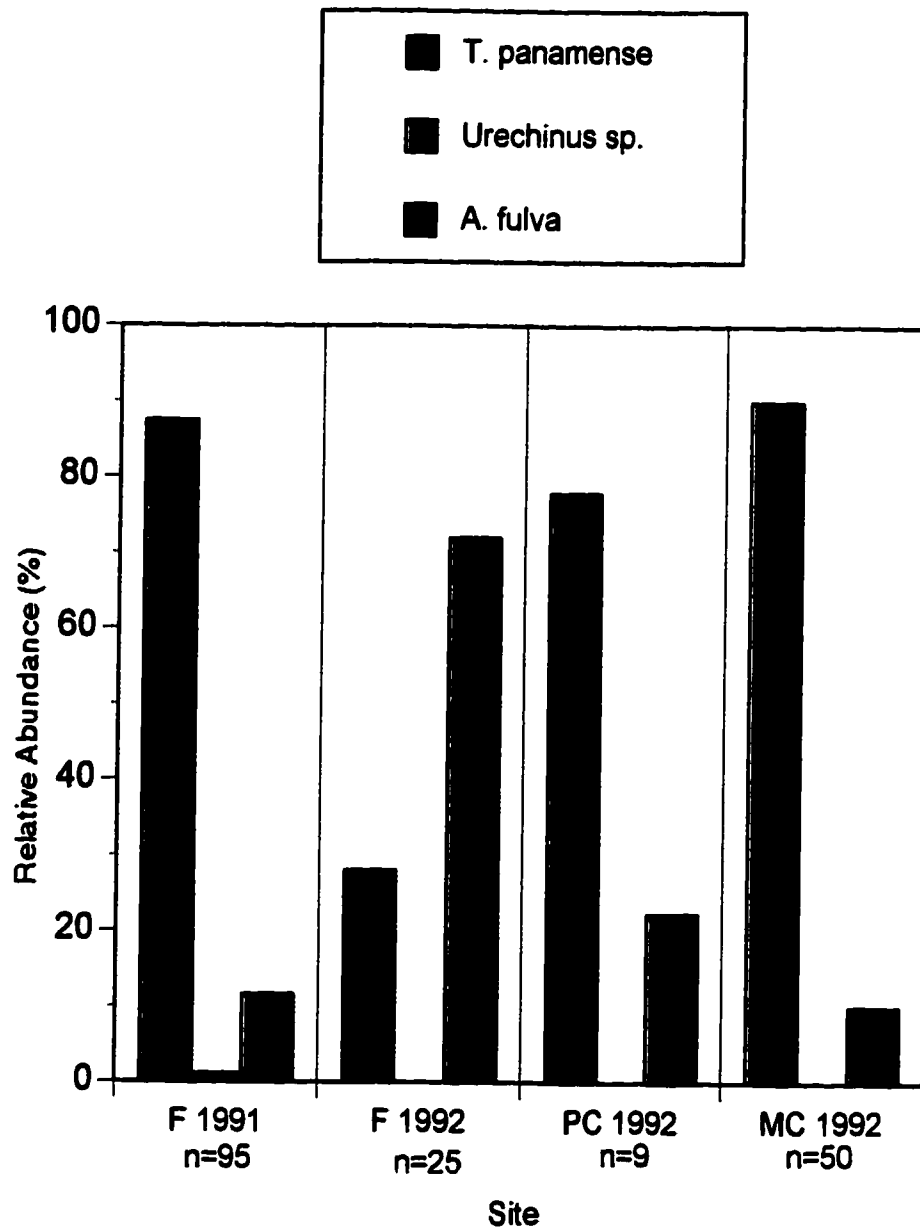


Figure 30. Comparison of the relative abundance of echinoid species collected with trawls at the Farallon 1991/1992, Pioneer Canyon, and Monterey Canyon study sites.

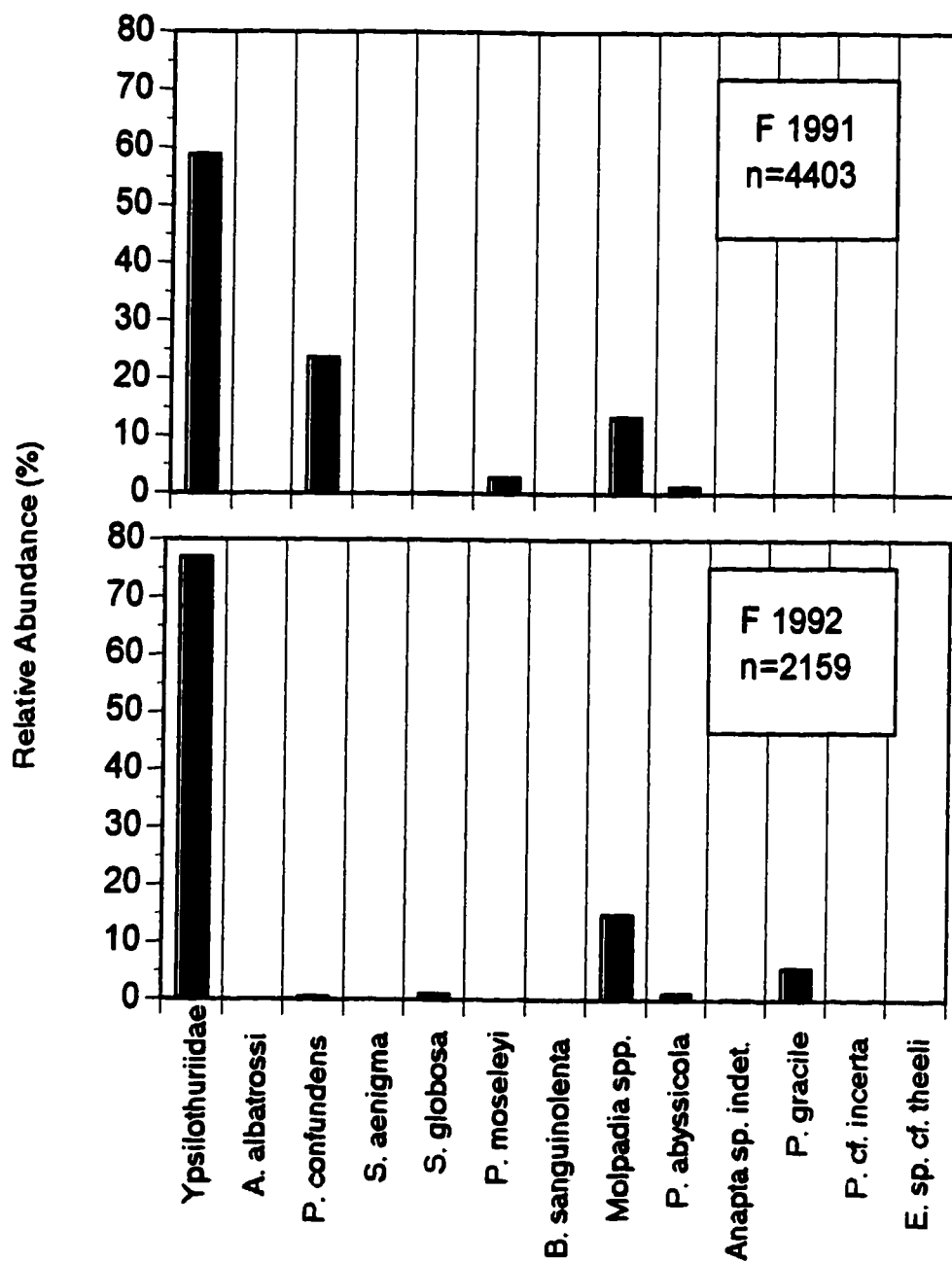


Figure 31. Comparison of the relative abundance of holothurian species collected with trawls at the Farallon site in 1991 and 1992.

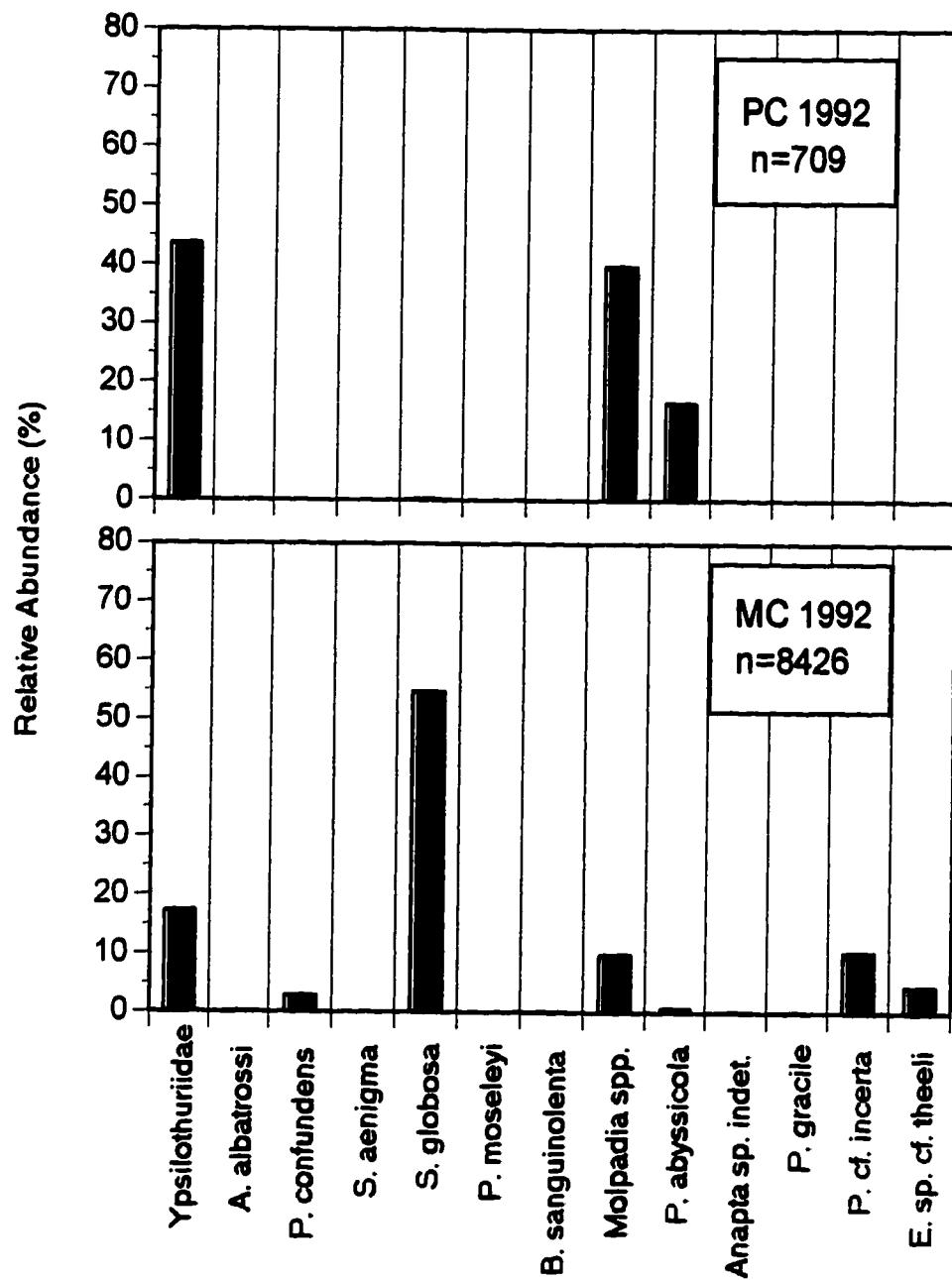


Figure 32. Comparison of the relative abundance of holothurian species collected with trawls at the Pioneer Canyon and Monterey Canyon sites.

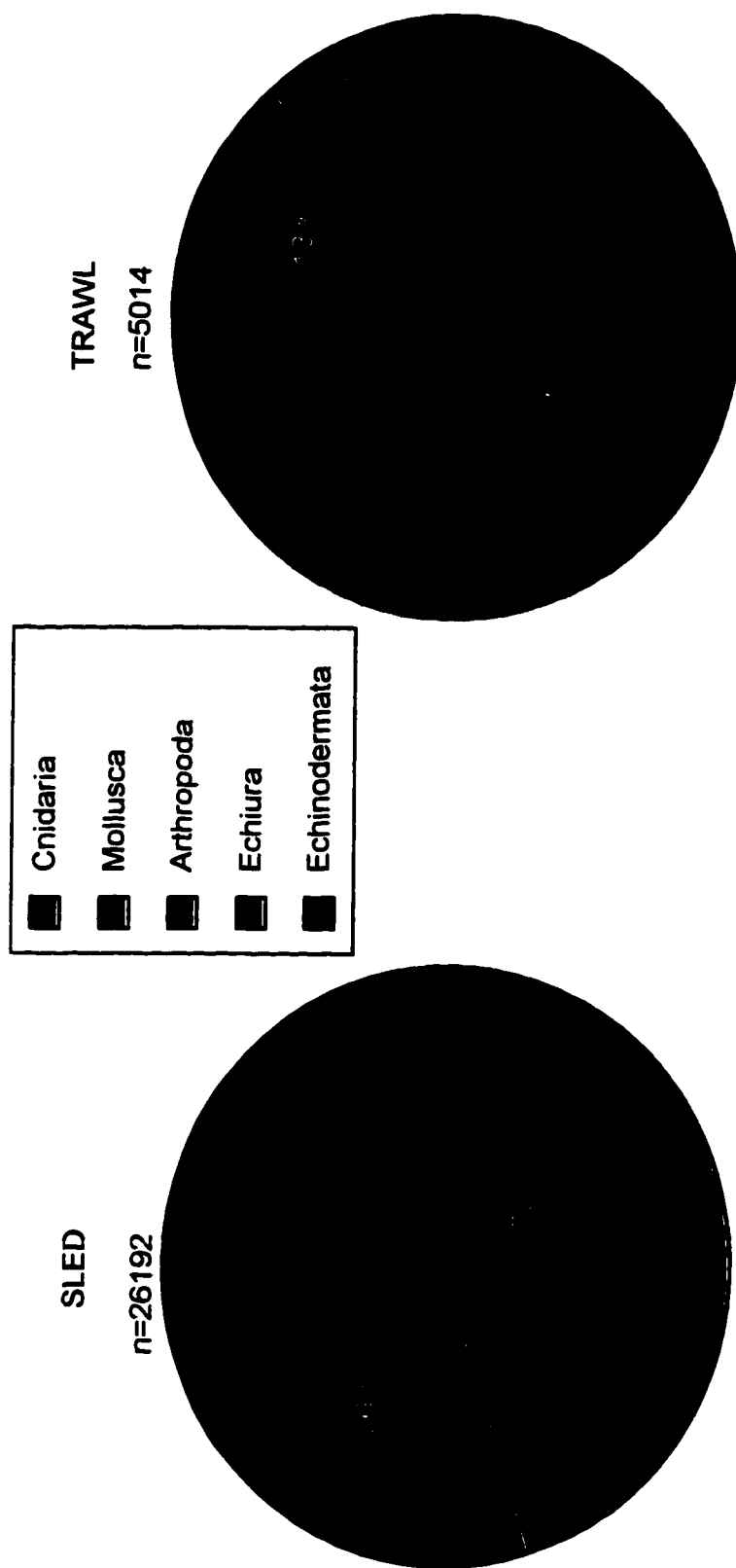


Figure 33. Pie charts showing the relative abundance of five major invertebrate phyla, trawls versus comparable camera sled segments at the Farallon 1991 site. (Annelida not shown because they are not discerned by the camera sled. Trawls #5 and #14 excluded because of no comparable camera sled segments.)

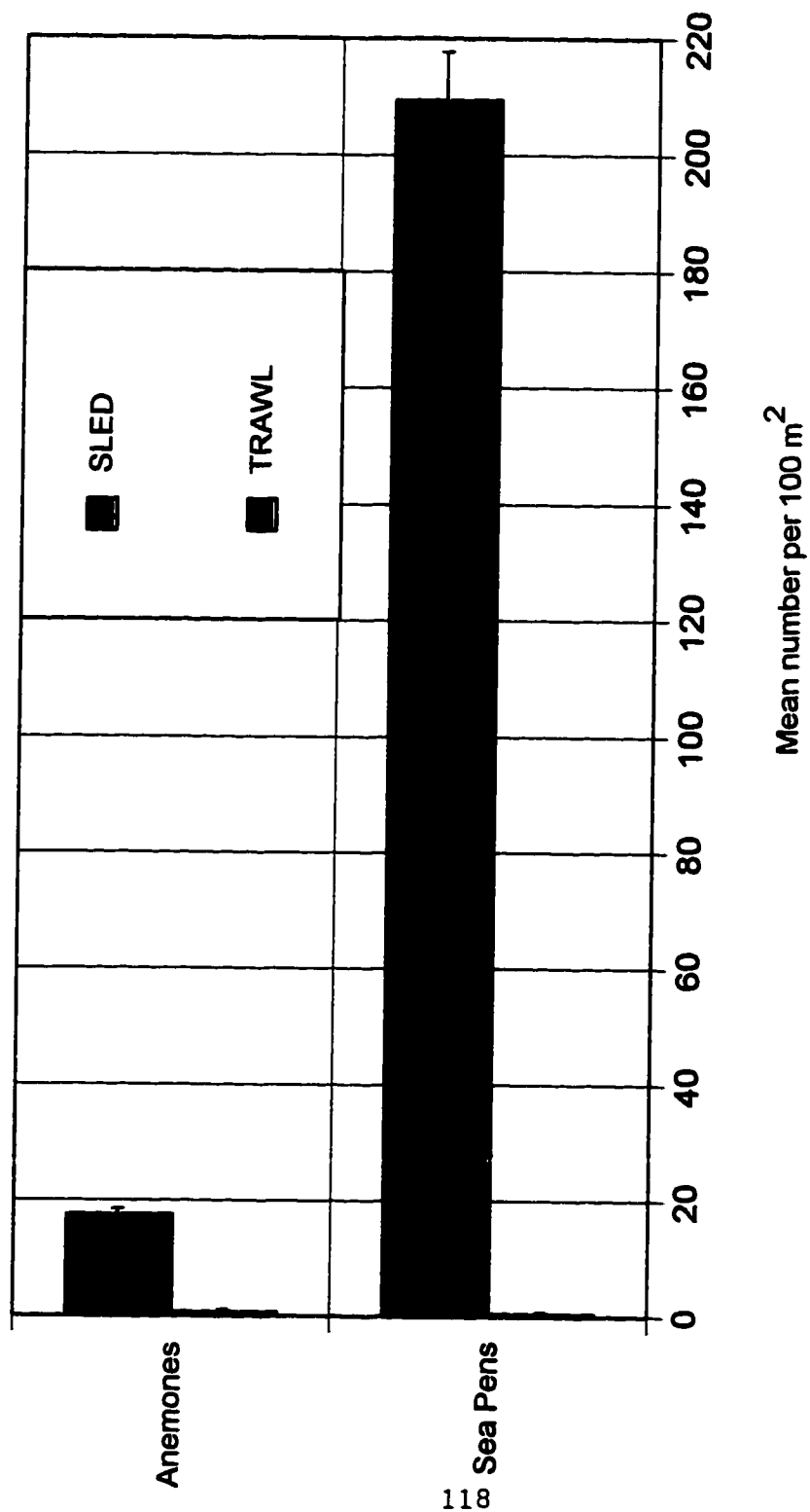


Figure 34. Comparison of the mean abundance of cnidarians (by order) per 100 m² (+/-SD) at the Farallon site in 1991, trawls versus comparable camera sled segments. (Other cnidarians excluded because of extremely low densities; actinians and corallimorpharians are combined in "anemones.")

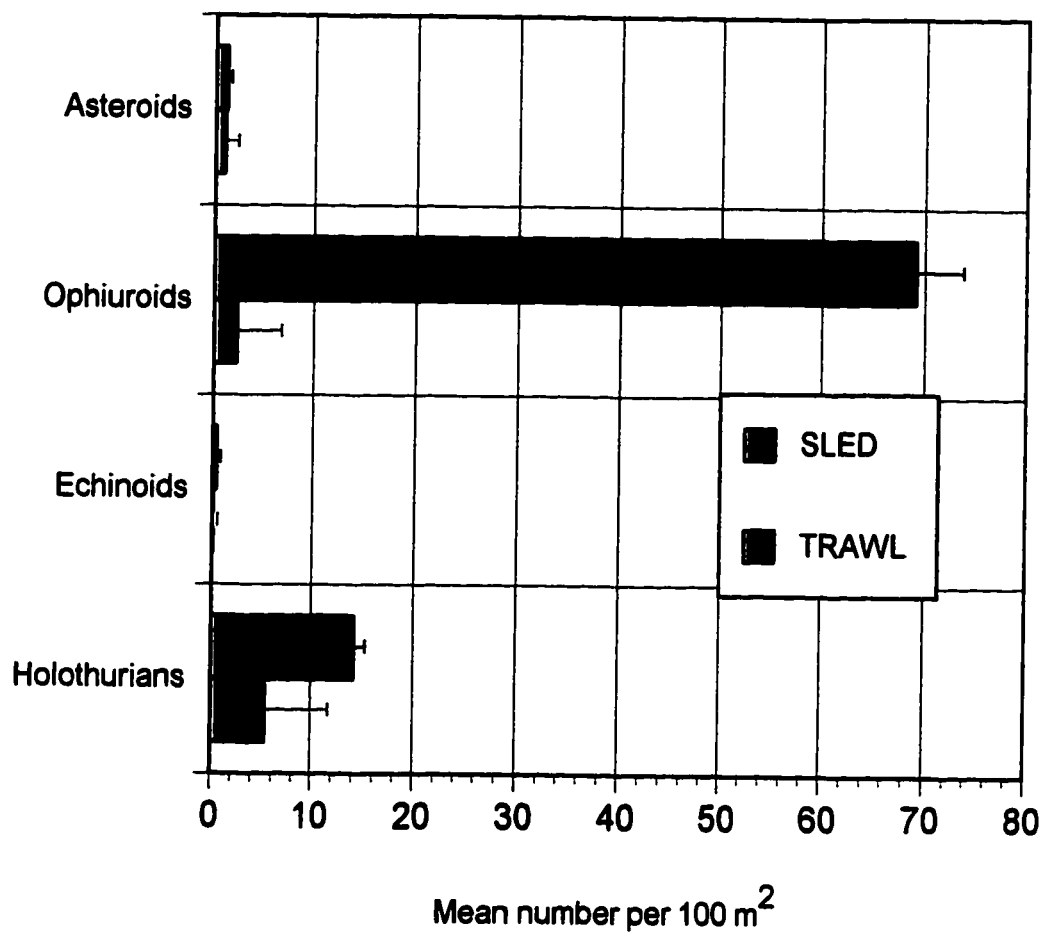


Figure 35. Comparison of the mean abundance of echinoderms (by class) per 100 m² (+/- SD) at the Farallon site in 1991, trawls versus comparable camera sled segments. (Crinoids excluded because of extremely low densities.)

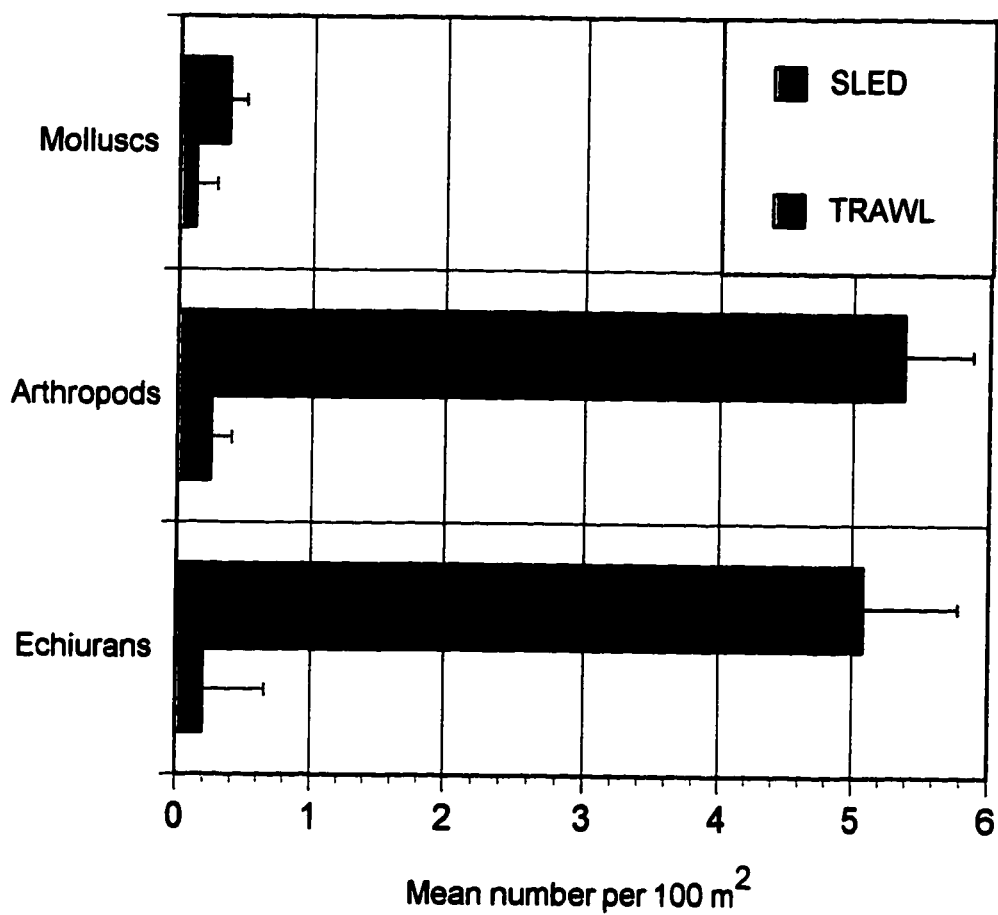


Figure 36. Comparison of the mean abundance of three phyla per 100 m² (+/-SD) at the Farallon site in 1991, trawls versus comparable camera sled segments.

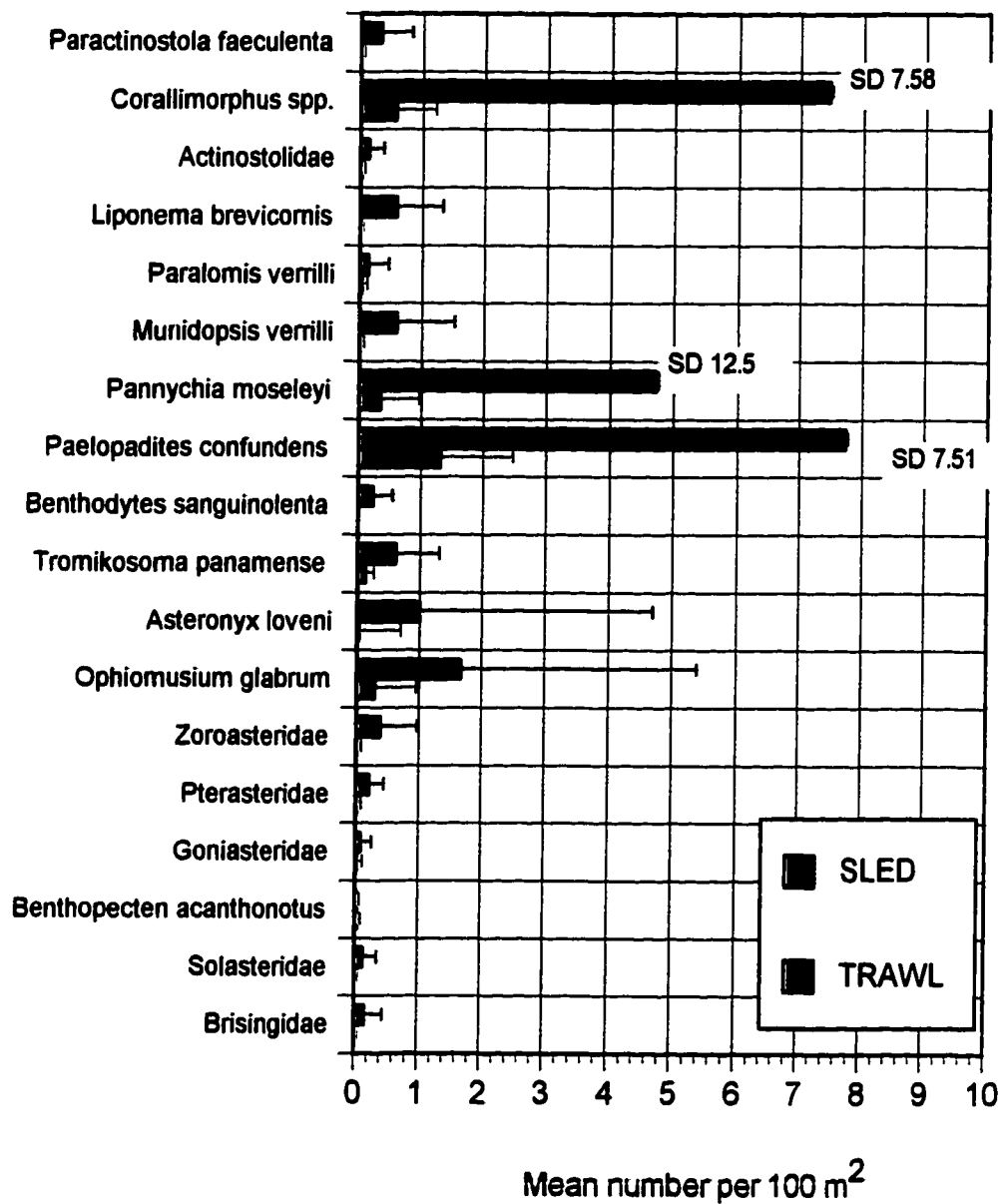
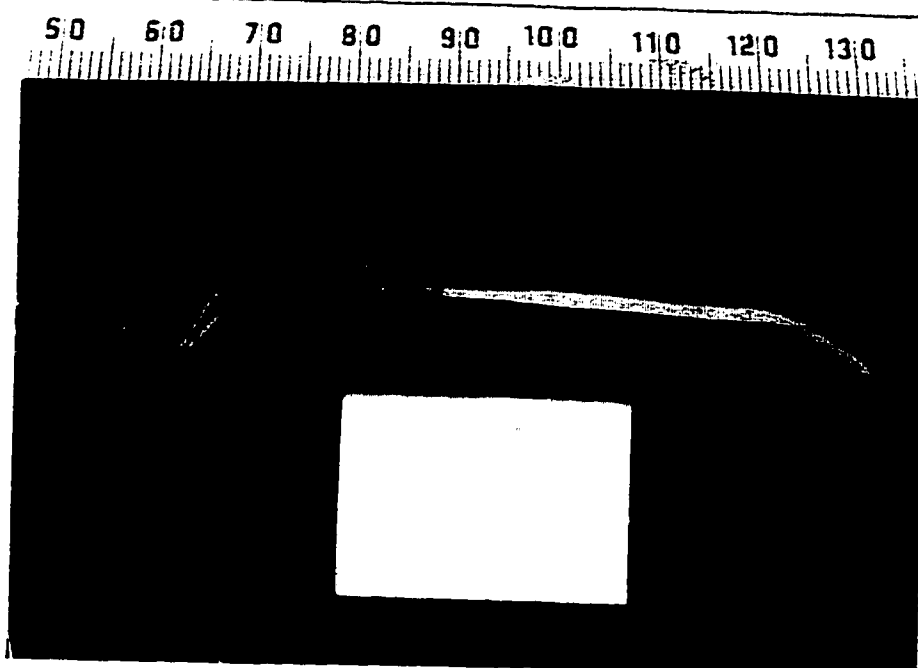


Figure 37. Mean abundance of comparable species/family, trawl versus equivalent camera sled segments (+/-SD).

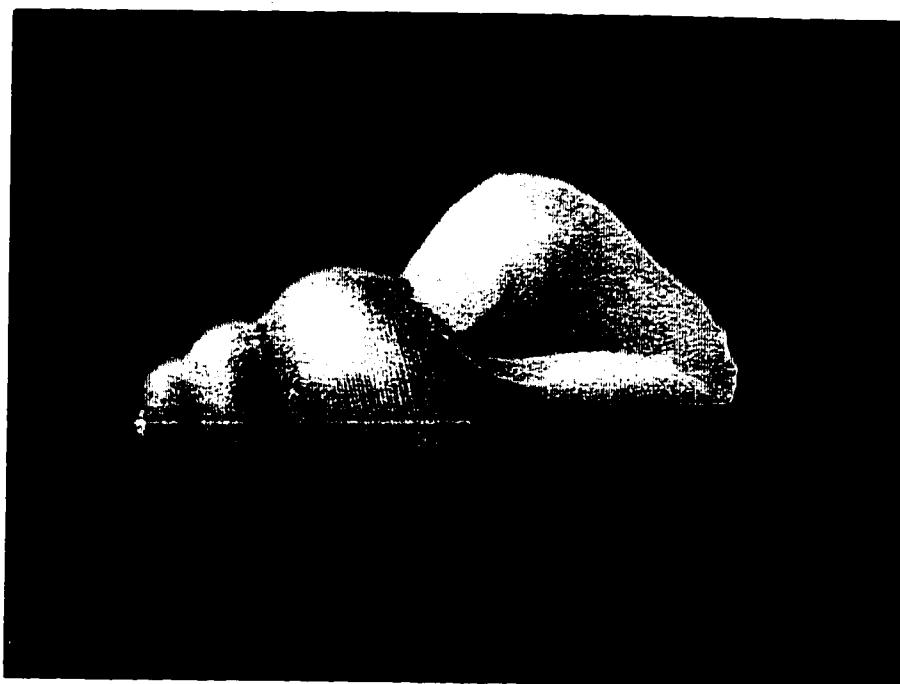
APPENDIX

- A. Photographs of trawled invertebrates from the Farallon site in the summer of 1991.
- B. Camera sled photographs from the Farallon site in the summer of 1991.

A1. The pennatulacean, Pennatula phosphorea.



A2. The gastropod, Colus jordani.



A3. The polyplacophoran, Leptochiton alveolus.



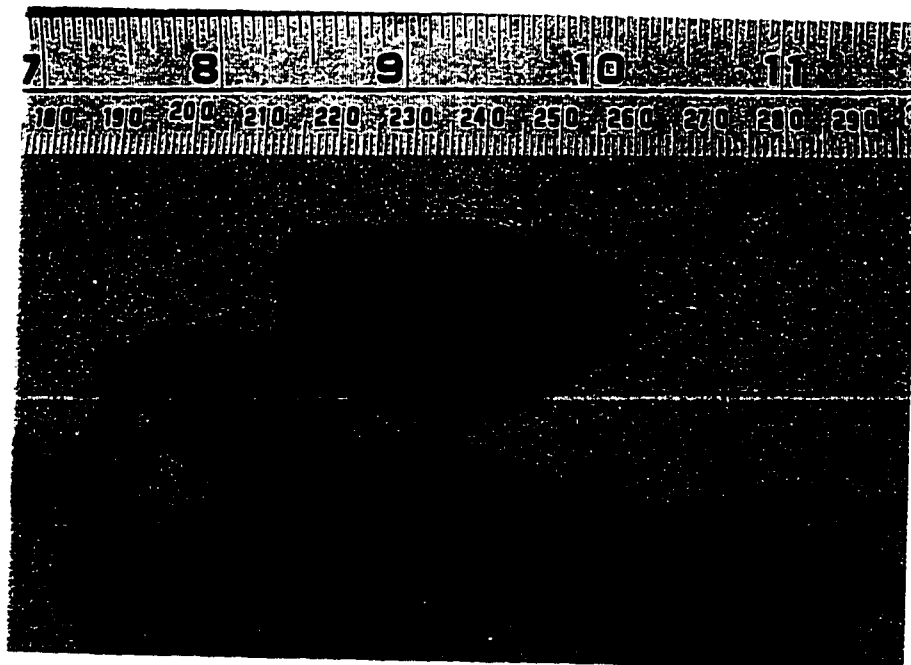
A4. The bivalve, Acharax johnsoni.



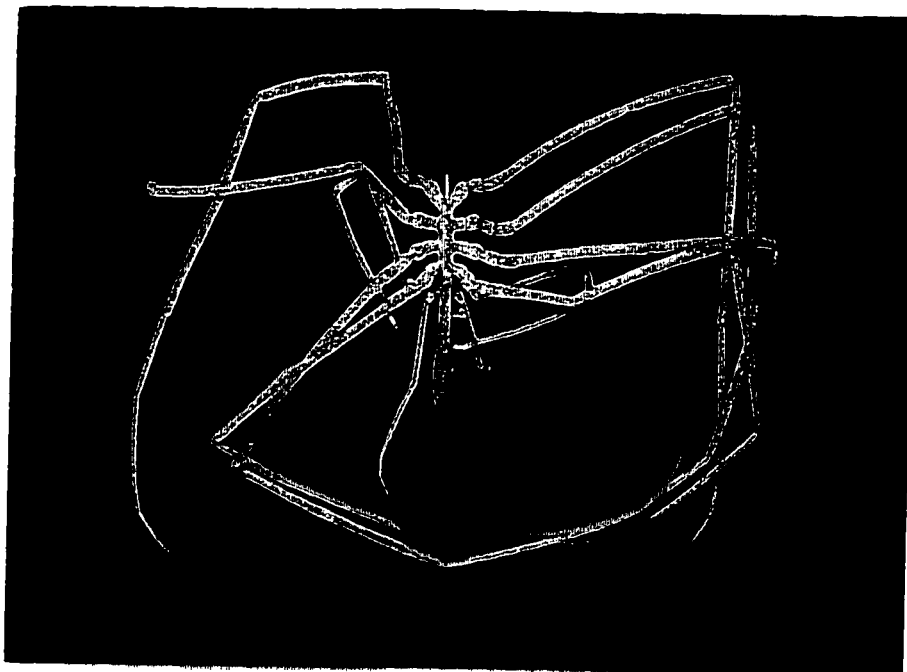
A5. The scaphopod, Fissidentalium megathyris.



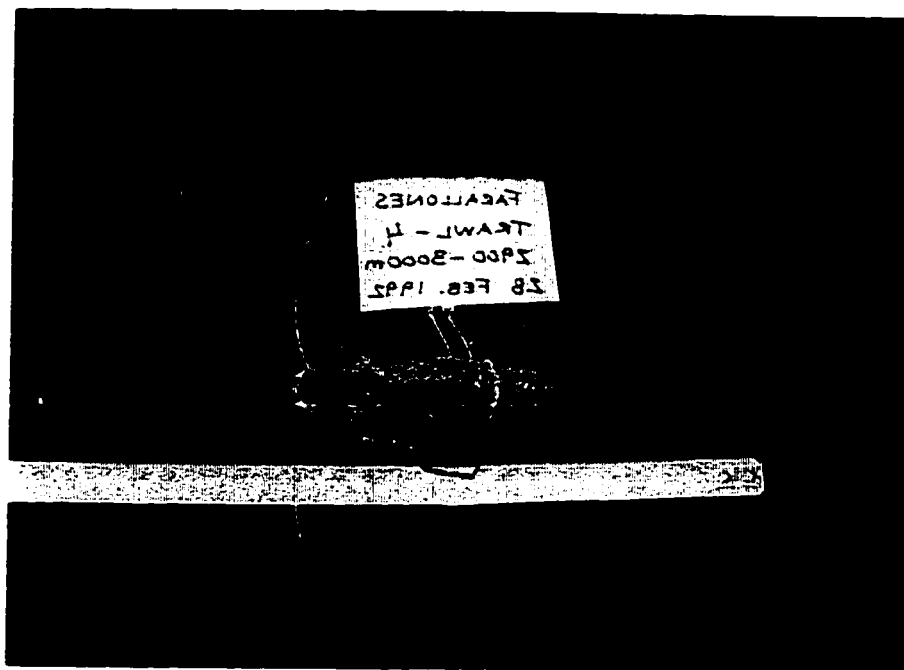
A6. The polychaete, Aphrodita cf. japonica.



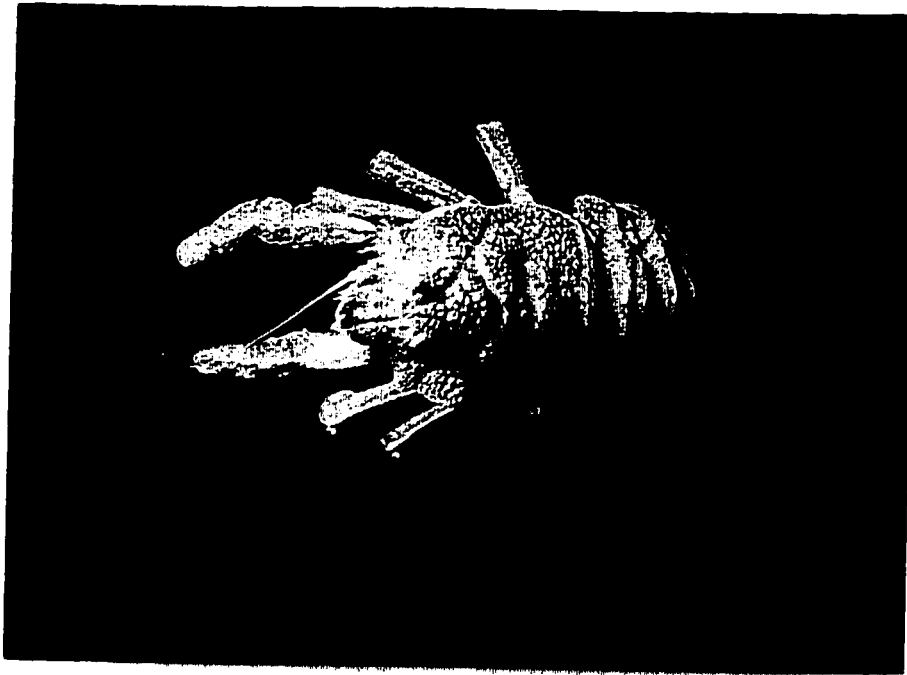
A7. The pycnogonid, Colossendeis sp. (colossea?).



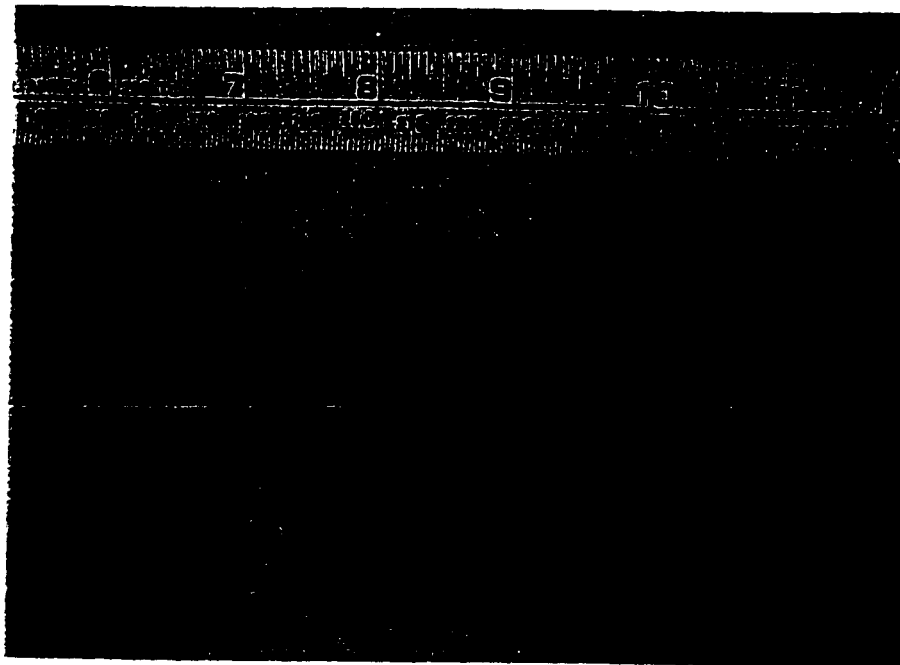
A8. The caridean shrimp, Crangon abyssorum.



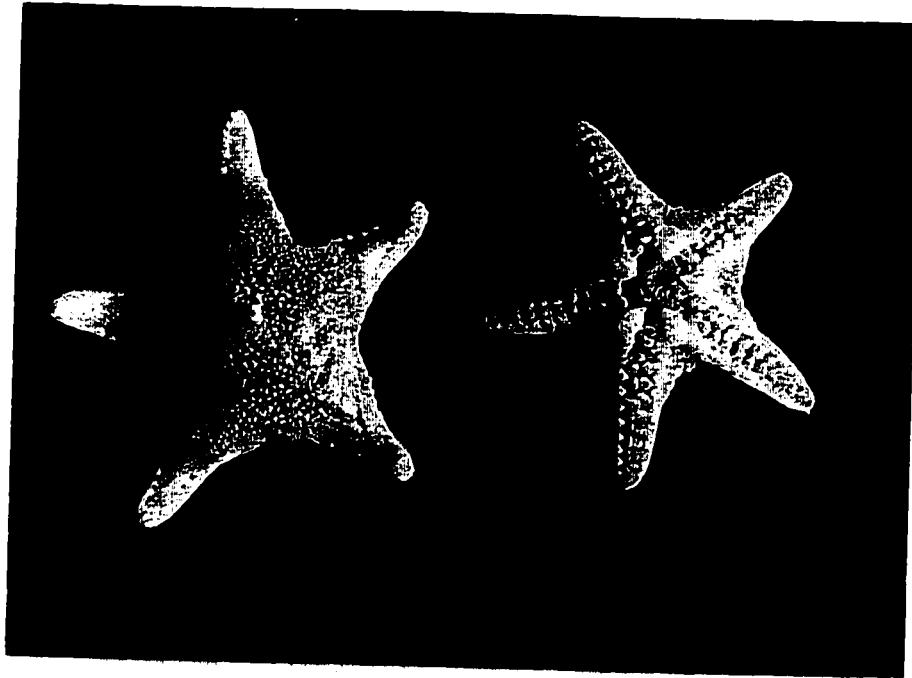
A9. The anomuran crab, Munidopsis verrilli.



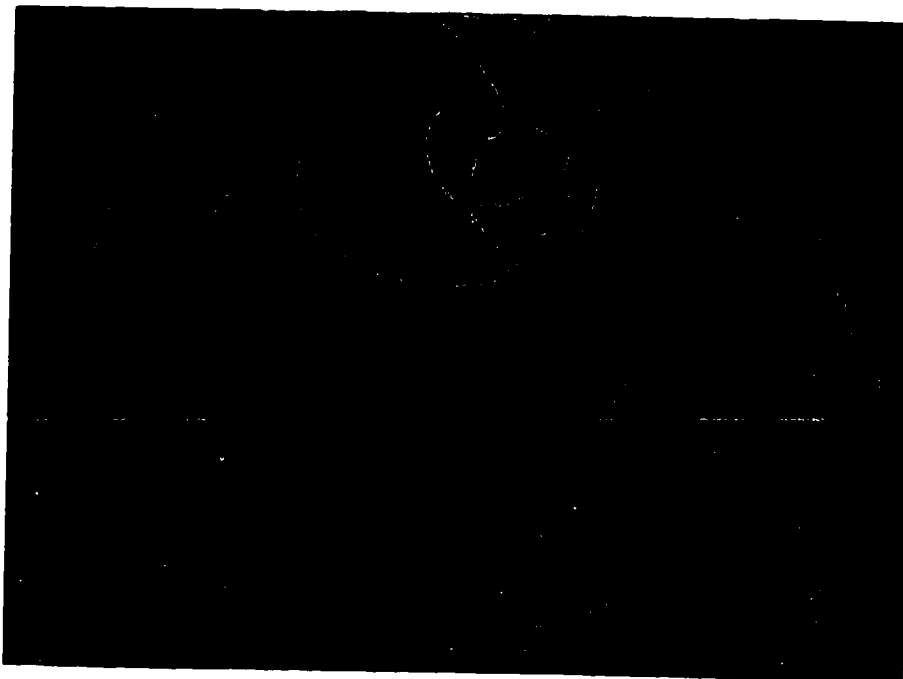
A10. The echiuran, Alomasoma nordpacificum.



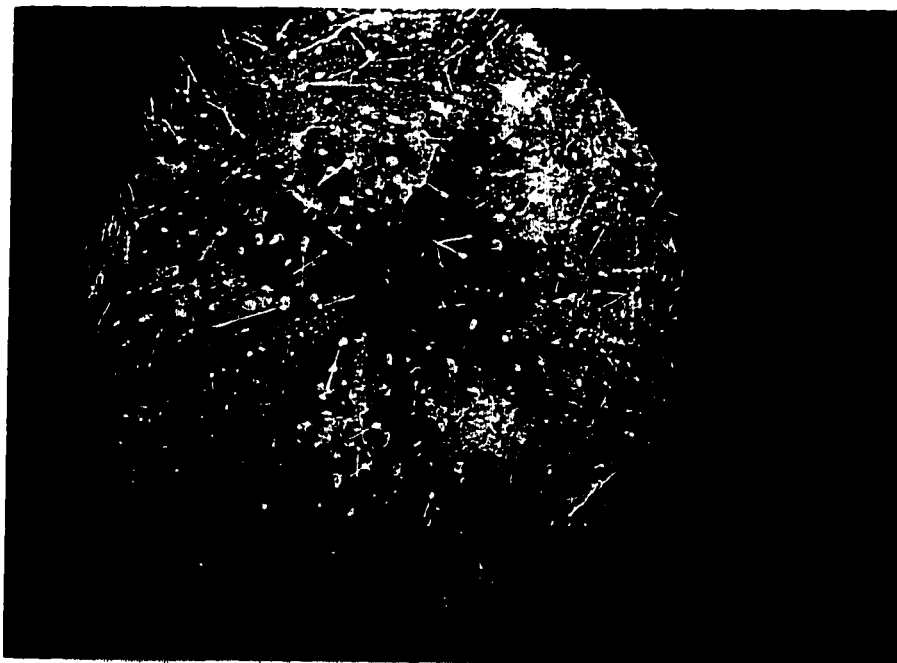
A11. The asteroid, Eremicaster pacificus.



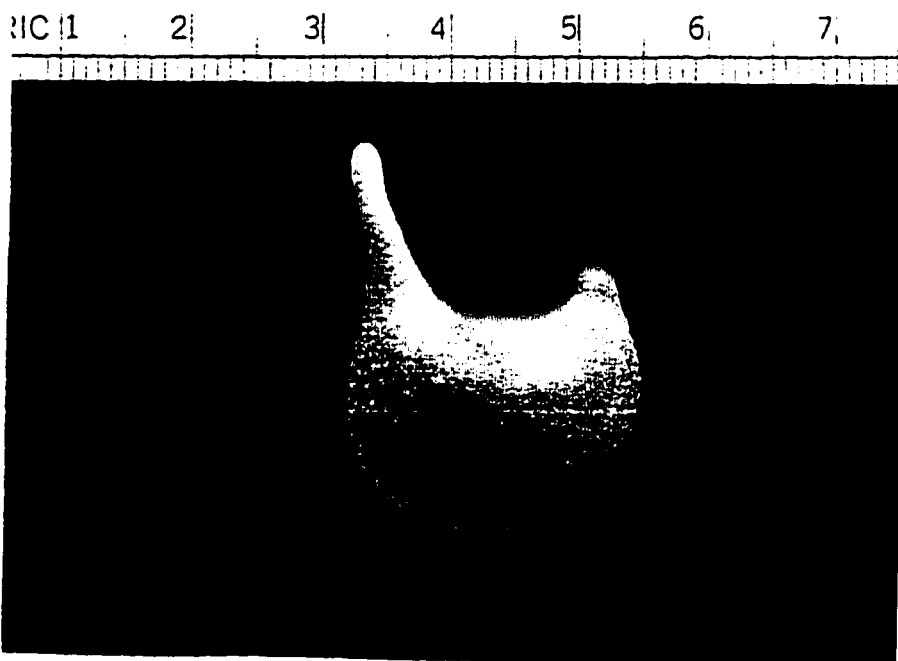
A12. The ophiuroid, Asteronyx loveni.



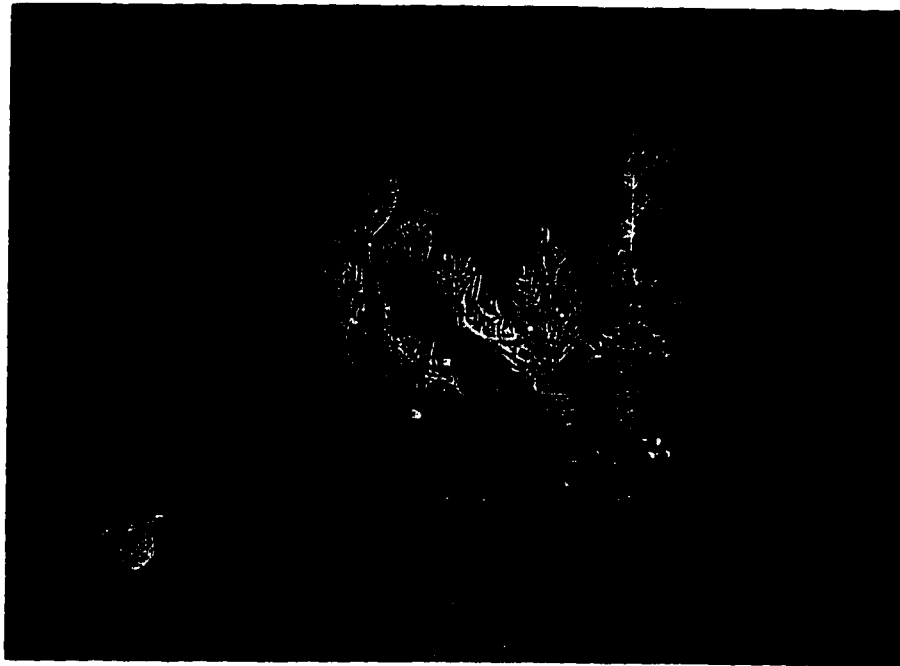
A13. The echinoid, Tromikosoma panamense.



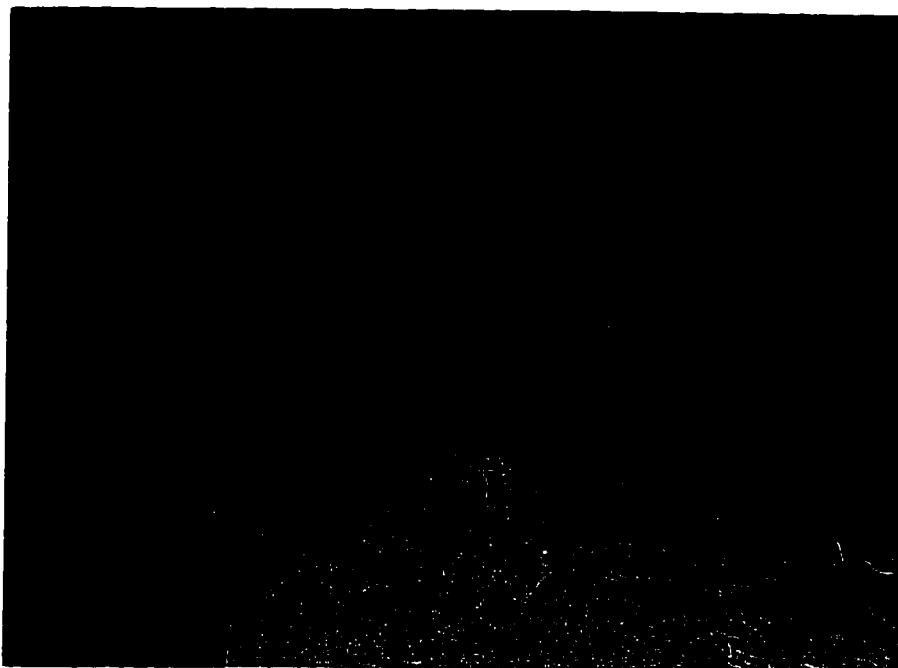
A14. A holothurian of the family Ypsilothuridae (either Ypsilothuria bitentaculata or Echinocucumis hispida).



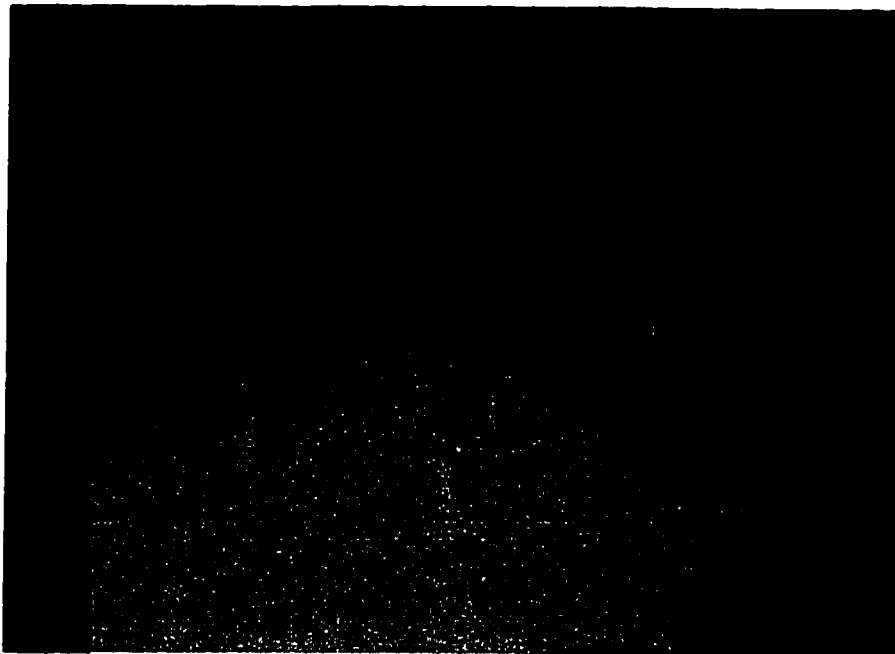
- B1. Unidentified anemones and gorgonians with associated ophiuroids (possibly Asteronyx loveni). Also note skate at far right.



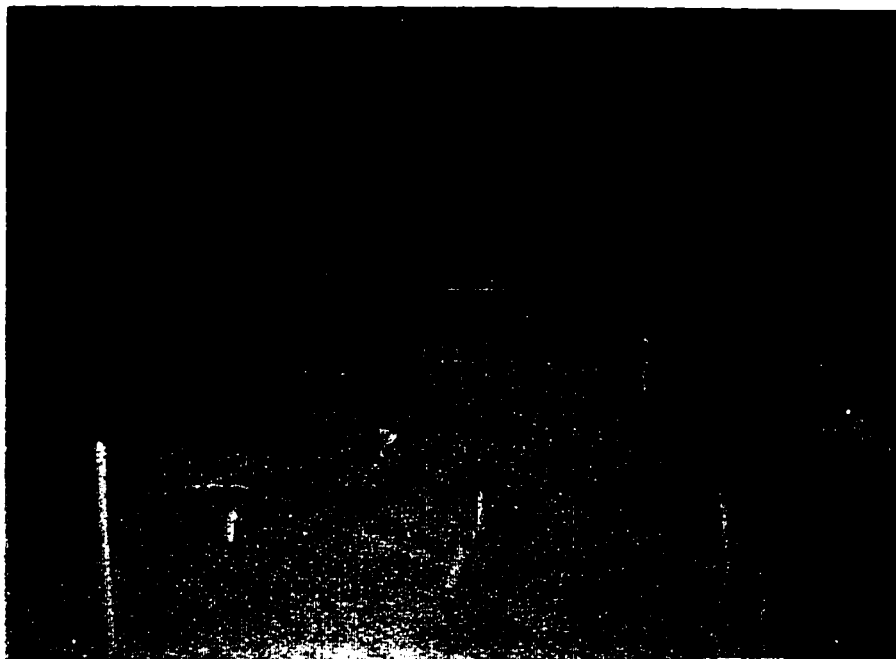
- B2. The "tumbleweed" anemone Liponema brevicornis, with the holothurian Scotoplanes globosa in the foreground.



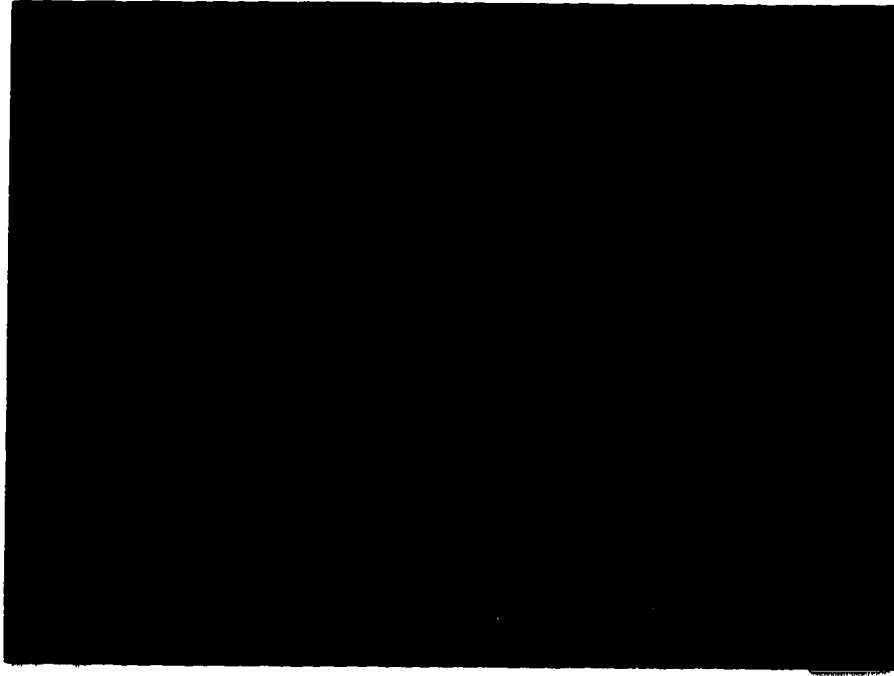
- B3. The corallimorpharian anemone Corallimorphus sp., and a number of pennatulaceans of the genus Kophobelemnion.



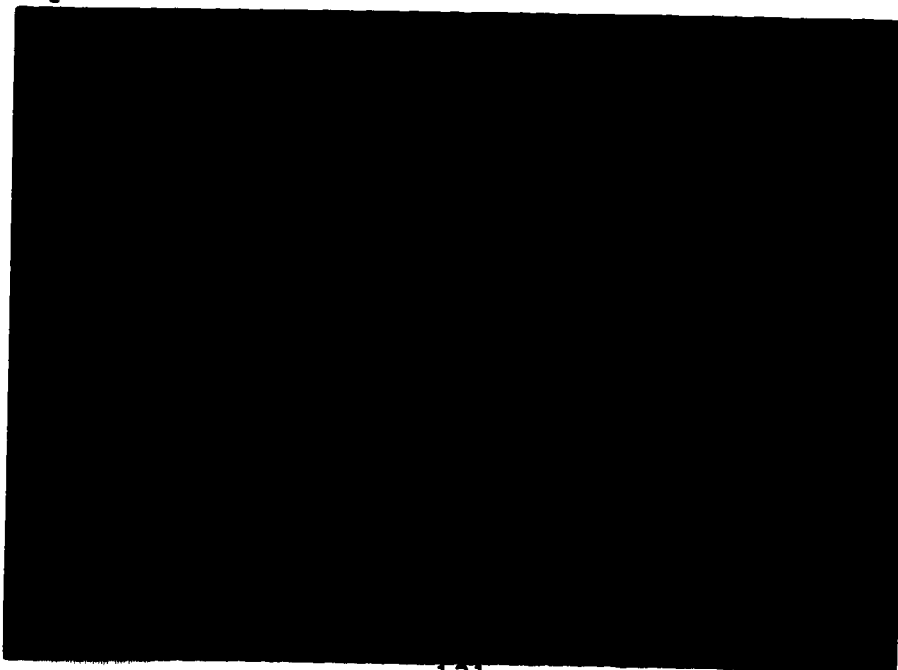
- B4. An octopod (possibly Graneledone pacifica), an unidentified shrimp, and unidentified ophiuroids. To the left of the shrimp are two specimens of the pennatulacean Pennatula phosphorea.



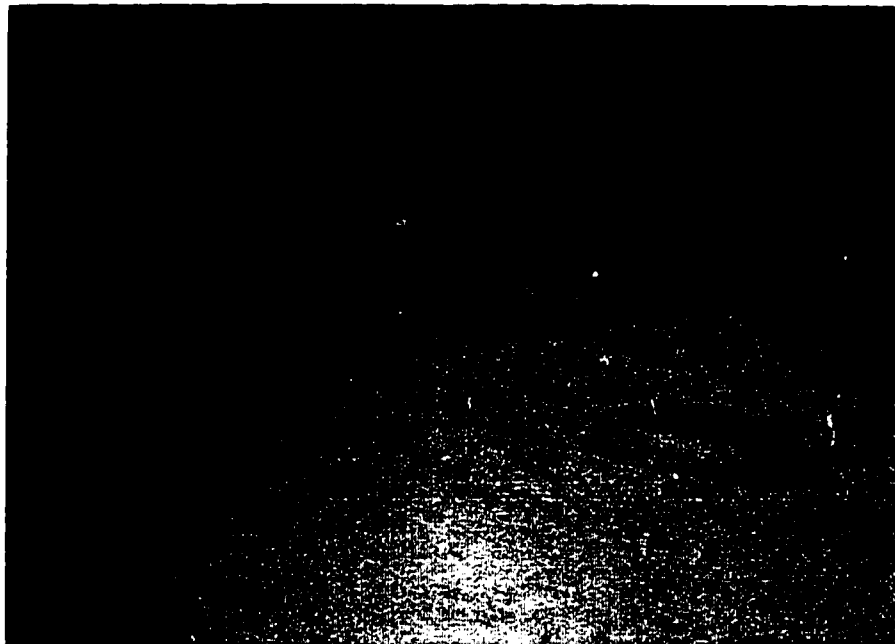
- B5. A large unidentified pycnogonid and pennatulaceans of the genus Kophobelemnion. Note the unidentified white ophiuroids at the bases of several of the sea pens.



- B6. An unidentified, dark green, extremely bifid echiuran only seen in camera sled photographs in areas of hard substrate. Note the alcyonacean Anthomastus ritteri on rocky area at upper left. Also unidentified ophiuroids.



- B7. The large, purple, benthopelagic holothurian Paelopadites confundens and the holothurian Pannychia moseleyi "rearing up." To the right of Paelopadites confundens is the sea pen Pennatula phosphorea.



- B8. A barren area devoid of epifaunal invertebrates.



- B9. Many small, grayish, nearly transparent specimens of elasipodid holothurians (probably Peniagone sp. or Elpidia sp. (This photograph was taken in Monterey Canyon in 1988 - no Peniagone or Elpidia were collected in trawls or seen in camera sled photographs at the Farallon site in 1991)).

